SEMESTER-I

UNIT-I

Virus

A **virus** is a submicroscopic infectious agent that replicates only inside the living cells of an organism.[1] Viruses infect all life forms, from animals and plants to microorganisms, including bacteria and archaea.[2][3] Viruses are found in almost every ecosystem on Earth and are the most numerous type of biological entity.[4][5] Since Dmitri Ivanovsky's 1892 article describing a non-bacterial pathogen infecting tobacco plants and the discovery of the tobacco mosaic virus by Martinus Beijerinck in 1898,[6]:4 more than 11,000 of the millions of virus species have been described in detail.[7][8] The study of viruses is known as virology, a subspeciality of microbiology.

When infected, a host cell is often forced to rapidly produce thousands of copies of the original virus. When not inside an infected cell or in the process of infecting a cell, viruses exist in the form of independent viral particles, or ***virions***, consisting of (i) genetic material, i.e., long molecules of DNA or RNA that encode the structure of the proteins by which the virus acts; (ii) a protein coat, the *capsid*, which surrounds and protects the genetic material; and in some cases (iii) an outside envelope of lipids. The shapes of these virus particles range from simple helical and icosahedral forms to more complex structures. Most virus species have virions too small to be seen with an optical microscope and are one-hundredth the size of most bacteria.

The origins of viruses in the evolutionary history of life are still unclear. Some viruses may have evolved from plasmids, which are pieces of DNA that can move between cells. Other viruses may have evolved from bacteria. In evolution, viruses are an important means of horizontal gene transfer, which increases genetic diversity in a way analogous to sexual reproduction.[9] Viruses are considered by some biologists to be a life form, because they carry genetic material, reproduce, and evolve through natural selection, although they lack some key characteristics, such as cell structure, that are generally considered necessary criteria for defining life. Because they possess some but not all such qualities, viruses have been described as "organisms at the edge of life"[10] and as replicators.[11]

Viruses spread in many ways. One transmission pathway is through disease-bearing organisms known as vectors: for example, viruses are often transmitted from plant to plant by insects that feed on plant sap, such as aphids; and viruses in animals can be carried by blood-sucking insects. Many viruses spread in the air by coughing and sneezing, including influenza viruses, SARS-CoV-2, chickenpox, smallpox, and measles. Norovirus and rotavirus, common causes of viral gastroenteritis, are transmitted by the faecal–oral route, passed by hand-to-mouth contact or in food or water. The infectious dose of norovirus required to produce infection in humans is fewer than 100 particles.[12] HIV is one of several viruses transmitted through sexual contact and by exposure to infected blood. The variety of host cells that a virus can

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infect is called its *host range*: this is *narrow* for viruses specialized to infect only a few species, or *broad* for viruses capable of infecting many.[13]: 123–124

Viral infections in animals provoke an immune response that usually eliminates the infecting virus. Immune responses can also be produced by vaccines, which confer an artificially acquired immunity to the specific viral infection. Some viruses, including those that cause HIV/AIDS, HPV infection, and viral hepatitis, evade these immune responses and result in chronic infections. Several classes of antiviral drugs have been developed.

Etymology

See also: Plural form of words ending in -us

The English word "virus" comes from the Latin *vīrus*, which refers to poison and other noxious liquids. *Vīrus* comes from the same Indo-European root as Sanskrit *viṣa*, Avestan *vīša*, and Ancient Greek ἰός (*iós*), which all mean "poison". The first attested use of "virus" in English appeared in 1398 in John Trevisa's translation of Bartholomeus Anglicus's *De Proprietatibus Rerum*.[14][15] *Virulent*, from Latin *virulentus* ('poisonous'), dates to c. 1400.[16][17] A meaning of 'agent that causes infectious disease' is first recorded in 1728,[15] long before the discovery of viruses by Dmitri Ivanovsky in 1892. The English plural is *viruses* (sometimes also *vira*),[18] whereas the Latin word is a mass noun, which has no classically attested plural (*vīra* is used in Neo-Latin[19]). The adjective *viral* dates to 1948.[20] The term *virion* (plural *virions*), which dates from 1959,[21] is also used to refer to a single viral particle that is released from the cell and is capable of infecting other cells of the same type.[22]

Origins

See also: Viral evolution

Viruses are found wherever there is life and have probably existed since living cells first evolved.[23] The origin of viruses is unclear because they do not form fossils, so molecular techniques are used to infer how they arose.[24] In addition, viral genetic material occasionally integrates into the germline of the host organisms, by which they can be passed on vertically to the offspring of the host for many generations. This provides an invaluable source of information for paleovirologists to trace back ancient viruses that existed as far back as millions of years ago.

There are three main hypotheses that aim to explain the origins of viruses:[25]

Regressive hypothesis

> Viruses may have once been small cells that parasitised larger cells. Over time, genes not required by their parasitism were lost. The bacteria rickettsia and chlamydia are living cells that, like viruses, can reproduce only inside host cells. They lend support to this hypothesis, as their dependence on parasitism is likely to have caused the loss of genes that enabled them to survive outside a cell. This is also called the "degeneracy hypothesis",[6]: 16[26]: 11 or "reduction hypothesis".[27]: 24

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Cellular origin hypothesis

Some viruses may have evolved from bits of DNA or RNA that "escaped" from the genes of a larger organism. The escaped DNA could have come from plasmids (pieces of naked DNA that can move between cells) or transposons (molecules of DNA that replicate and move around to different positions within the genes of the cell).[13]:810 Once called "jumping genes", transposons are examples of mobile genetic elements and could be the origin of some viruses. They were discovered in maize by Barbara McClintock in 1950.[28] This is sometimes called the "vagrancy hypothesis",[6]:16[26]:11–12 or the "escape hypothesis".[27]:24

Co-evolution hypothesis

This is also called the "virus-first hypothesis"[27]:24 and proposes that viruses may have evolved from complex molecules of protein and nucleic acid at the same time that cells first appeared on Earth and would have been dependent on cellular life for billions of years. Viroids are molecules of RNA that are not classified as viruses because they lack a protein coat. They have characteristics that are common to several viruses and are often called subviral agents.[6]:55 Viroids are important pathogens of plants.[13]:791 They do not code for proteins but interact with the host cell and use the host machinery for their replication.[29] The hepatitis delta virus of humans has an RNA genome similar to viroids but has a protein coat derived from hepatitis B virus and cannot produce one of its own. It is, therefore, a defective virus. Although hepatitis delta virus genome may replicate independently once inside a host cell, it requires the help of hepatitis B virus to provide a protein coat so that it can be transmitted to new cells.[13]:460 In similar manner, the sputnik virophage is dependent on mimivirus, which infects the protozoan *Acanthamoeba castellanii*.[30] These viruses, which are dependent on the presence of other virus species in the host cell, are called "satellites" and may represent evolutionary intermediates of viroids and viruses.[26]:777>[6]:55–57

In the past, there were problems with all of these hypotheses: the regressive hypothesis did not explain why even the smallest of cellular parasites do not resemble viruses in any way. The escape hypothesis did not explain the complex capsids and other structures on virus particles. The virus-first hypothesis contravened the definition of viruses in that they require host cells.[27]:24 Viruses are now recognised as ancient and as having origins that pre-date the divergence of life into the three domains.[27]:28 This discovery has led modern virologists to reconsider and re-evaluate these three classical hypotheses.[27]:28

The evidence for an ancestral world of RNA cells[27]:26 and computer analysis of viral and host DNA sequences give a better understanding of the evolutionary relationships between different viruses and may help identify the ancestors of modern viruses. To date, such analyses have not proved which of these hypotheses is correct.[27]:26 It seems unlikely that all currently known viruses have a common ancestor, and viruses have probably arisen numerous times in the past by one or more mechanisms.[31]

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Microbiology

Discovery

Main article: History of virology

The first evidence of the existence of viruses came from experiments with filters that had pores small enough to retain bacteria. In 1892, Dmitri Ivanovsky used one of these filters to show that sap from a diseased tobacco plant remained infectious to healthy tobacco plants despite having been filtered. Martinus Beijerinck called the filtered, infectious substance a "virus" and this discovery is considered to be the beginning of virology. The subsequent discovery and partial characterization of bacteriophages by Frederick Twort and Félix d'Herelle further catalyzed the field, and by the early 20th century many viruses had been discovered. In 1926, Thomas Milton Rivers defined viruses as obligate parasites. Viruses were demonstrated to be particles, rather than a fluid, by Wendell Meredith Stanley, and the invention of the electron microscope in 1931 allowed their complex structures to be visualised.[32]

Life properties

Scientific opinions differ on whether viruses are a form of life or organic structures that interact with living organisms.[11] They have been described as "organisms at the edge of life",[10] since they resemble organisms in that they possess genes, evolve by natural selection,[33] and reproduce by creating multiple copies of themselves through self-assembly. Although they have genes, they do not have a cellular structure, which is often seen as the basic unit of life. Viruses do not have their own metabolism and require a host cell to make new products. They therefore cannot naturally reproduce outside a host cell[34]—although some bacteria such as rickettsia and chlamydia are considered living organisms despite the same limitation.[35][36] Accepted forms of life use cell division to reproduce, whereas viruses spontaneously assemble within cells. They differ from autonomous growth of crystals as they inherit genetic mutations while being subject to natural selection. Virus self-assembly within host cells has implications for the study of the origin of life, as it lends further credence to the hypothesis that life could have started as self-assembling organic molecules.[2] The virocell model first proposed by Patrick Forterre considers the infected cell to be the "living form" of viruses and that virus particles (virions) are analogous to spores.[37] Although the living versus non-living debate continues, the virocell model has gained some acceptance.[38]

Structure

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Virions of some of the most common human viruses with their relative size. The nucleic acids are not to scale.

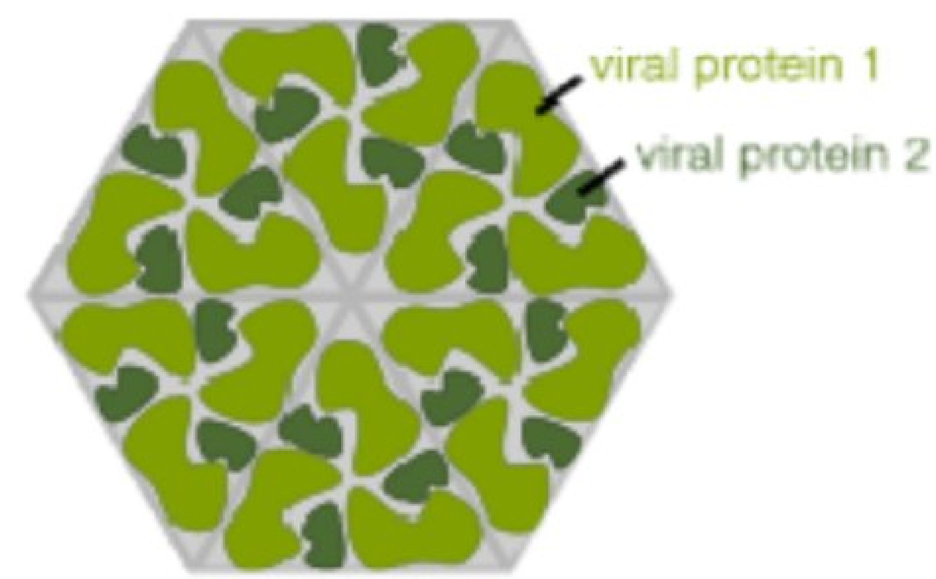
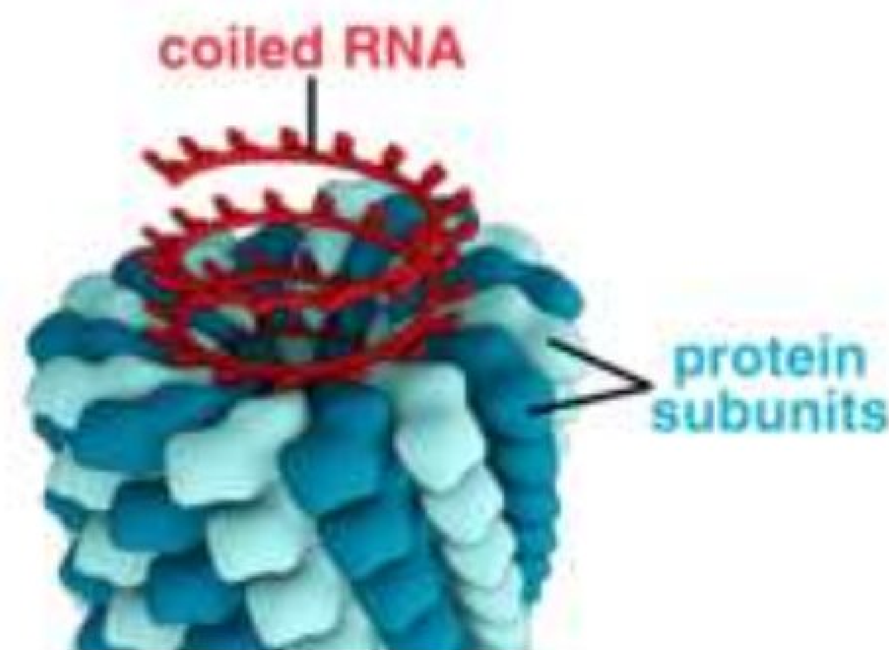
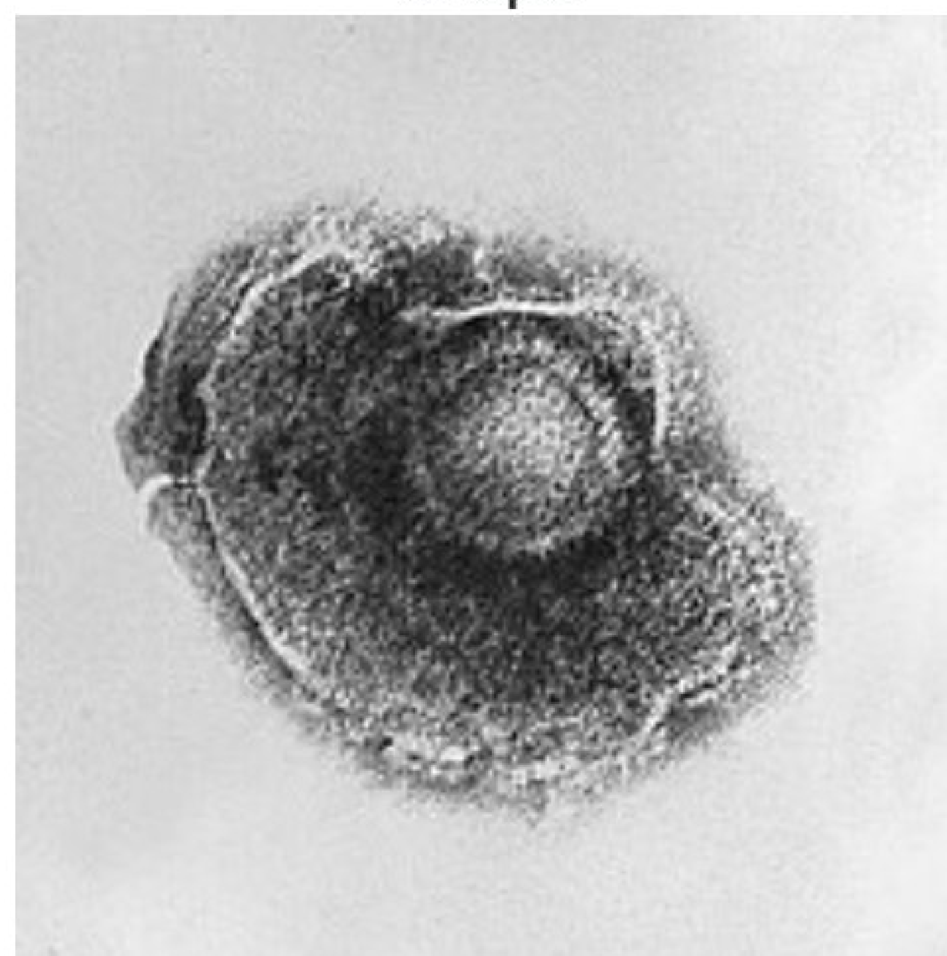


Diagram of how a virus capsid can be constructed using multiple copies of just two protein molecules



Structure of tobacco mosaic virus: RNA coiled in a helix of repeating protein sub-units

Structure of icosahedral adenovirus. Electron micrograph with an illustration to show shape



Structure of chickenpox virus. They have a lipid envelope.

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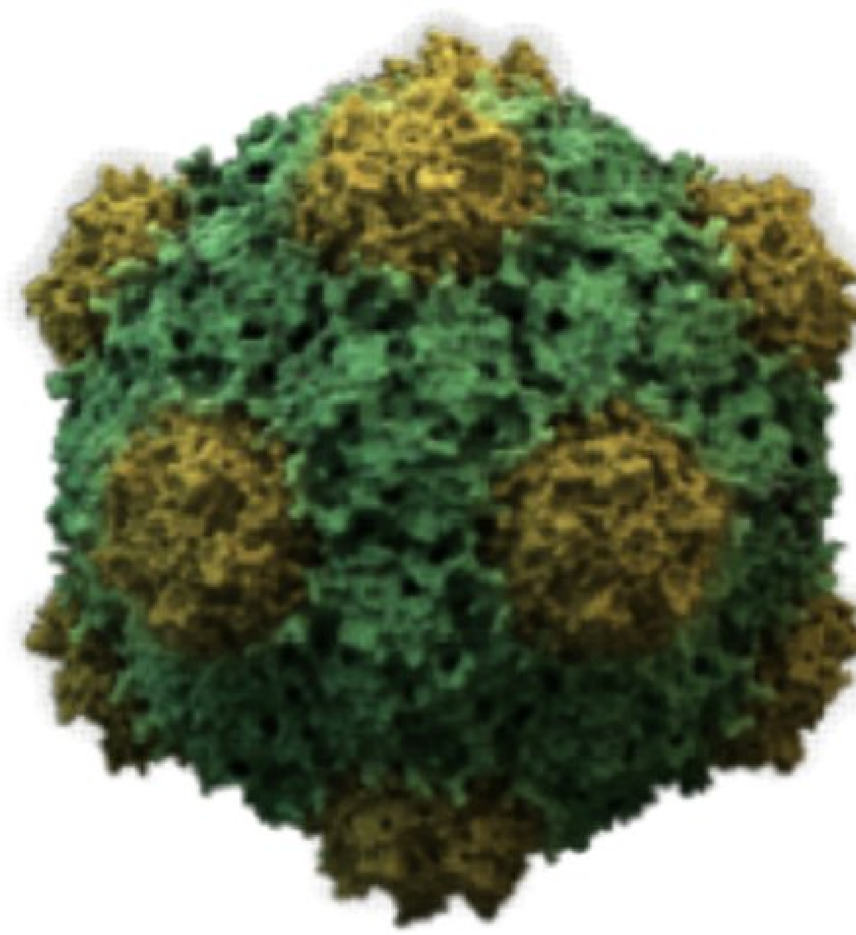
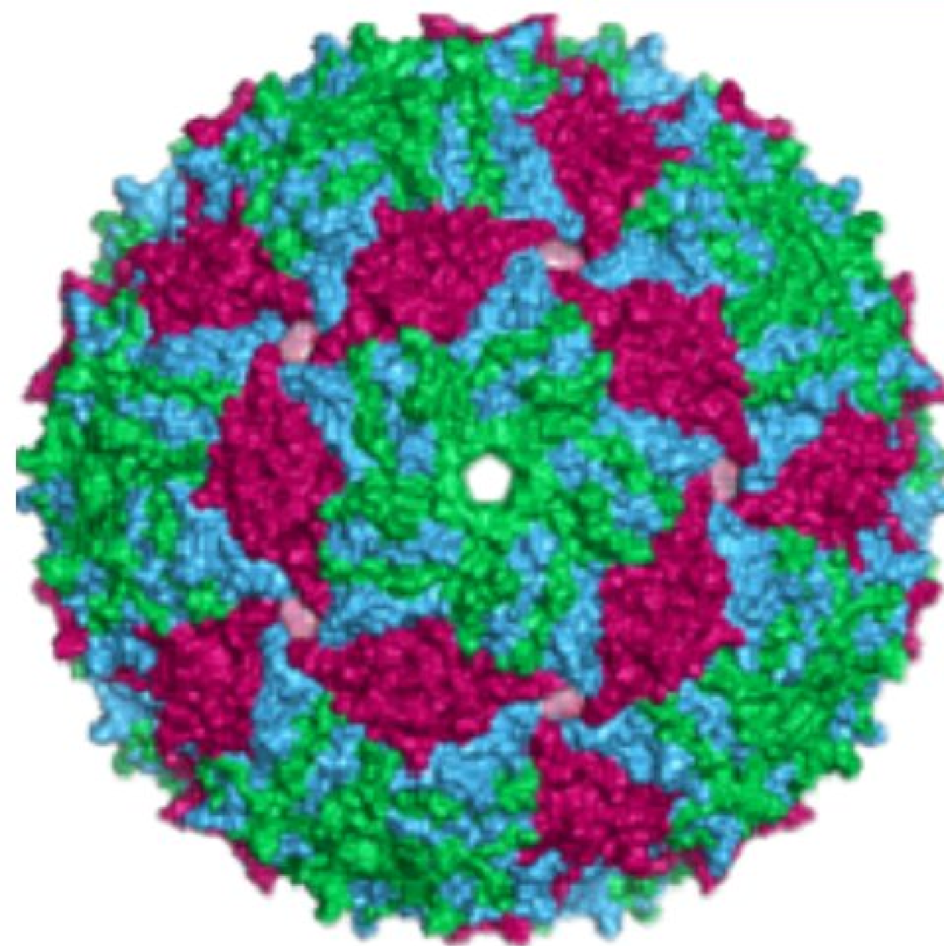


Structure of an icosahedral cowpea mosaic virus



Bacteriophage Escherichia virus MS2 capsid. This spherical virus also has icosahedral symmetry.

Viruses display a wide diversity of sizes and shapes, called 'morphologies'. In general, viruses are much smaller than bacteria and more than a thousand bacteriophage viruses would fit inside an *Escherichia coli* bacterium's cell.[39]:98 Many viruses that have been studied are spherical and have a diameter between 20 and 300 nanometres. Some filoviruses, which are filaments, have a total length of up to 1400 nm; their diameters are only about 80 nm.[26]:33–55 Most viruses cannot be seen with an optical microscope, so scanning and transmission electron microscopes are used to visualise them.[26]:33–37 To increase the contrast between viruses and the background, electron-dense "stains" are used. These are solutions of salts of heavy metals, such as tungsten, that scatter the electrons from regions covered with the stain. When virions are coated with stain (positive staining), fine detail is obscured. Negative staining overcomes this problem by staining the background only.[40]

A complete virus particle, known as a *virion*, consists of nucleic acid surrounded by a protective coat of protein called a capsid. These are formed from protein subunits called capsomeres.[26]:40 Viruses can have a lipid "envelope" derived from the host cell membrane. The capsid is made from proteins encoded by the viral genome and its shape serves as the basis for morphological distinction.[41][42] Virally-coded protein subunits will self-assemble to form a capsid, in general requiring the presence of the virus

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genome. Complex viruses code for proteins that assist in the construction of their capsid. Proteins associated with nucleic acid are known as nucleoproteins, and the association of viral capsid proteins with viral nucleic acid is called a nucleocapsid. The capsid and entire virus structure can be mechanically (physically) probed through atomic force microscopy.[43][44] In general, there are five main morphological virus types:

Helical

These viruses are composed of a single type of capsomere stacked around a central axis to form a helical structure, which may have a central cavity, or tube. This arrangement results in virions which can be short and highly rigid rods, or long and very flexible filaments. The genetic material (typically single-stranded RNA, but single-stranded DNA in some cases) is bound into the protein helix by interactions between the negatively charged nucleic acid and positive charges on the protein. Overall, the length of a helical capsid is related to the length of the nucleic acid contained within it, and the diameter is dependent on the size and arrangement of capsomeres. The well-studied tobacco mosaic virus[26]:37 and inovirus[45] are examples of helical viruses.

Icosahedral

Most animal viruses are icosahedral or near-spherical with chiral icosahedral symmetry. A regular icosahedron is the optimum way of forming a closed shell from identical subunits. The minimum number of capsomeres required for each triangular face is 3, which gives 60 for the icosahedron. Many viruses, such as rotavirus, have more than 60 capsomers and appear spherical but they retain this symmetry. To achieve this, the capsomeres at the apices are surrounded by five other capsomeres and are called pentons. Capsomeres on the triangular faces are surrounded by six others and are called hexons.[26]:40,42 Hexons are in essence flat and pentons, which form the 12 vertices, are curved. The same protein may act as the subunit of both the pentamers and hexamers or they may be composed of different proteins.[46]

Prolate

This is an icosahedron elongated along the fivefold axis and is a common arrangement of the heads of bacteriophages. This structure is composed of a cylinder with a cap at either end.[47]

Enveloped

Some species of virus envelop themselves in a modified form of one of the cell membranes, either the outer membrane surrounding an infected host cell or internal membranes such as a nuclear membrane or endoplasmic reticulum, thus gaining an outer lipid bilayer known as a viral envelope. This membrane is studded with proteins coded for by the viral genome and host genome; the lipid membrane itself and any carbohydrates present originate entirely from the host. Influenza virus, HIV (which causes AIDS), and severe acute respiratory syndrome coronavirus 2 (which causes COVID-19)[48] use this strategy. Most enveloped viruses are dependent on the envelope for their infectivity.[26]:42–43

Complex

These viruses possess a capsid that is neither purely helical nor purely icosahedral, and that may possess extra structures such as protein tails or a

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complex outer wall. Some bacteriophages, such as Enterobacteria phage T4, have a complex structure consisting of an icosahedral head bound to a helical tail, which may have a hexagonal base plate with protruding protein tail fibres. This tail structure acts like a molecular syringe, attaching to the bacterial host and then injecting the viral genome into the cell.[49]

The poxviruses are large, complex viruses that have an unusual morphology. The viral genome is associated with proteins within a central disc structure known as a nucleoid. The nucleoid is surrounded by a membrane and two lateral bodies of unknown function. The virus has an outer envelope with a thick layer of protein studded over its surface. The whole virion is slightly pleomorphic, ranging from ovoid to brick-shaped.[50]

Giant viruses

Main article: Giant virus

Mimivirus is one of the largest characterised viruses, with a capsid diameter of 400 nm. Protein filaments measuring 100 nm project from the surface. The capsid appears hexagonal under an electron microscope, therefore the capsid is probably icosahedral.[51] In 2011, researchers discovered the largest then known virus in samples of water collected from the ocean floor off the coast of Las Cruces, Chile. Provisionally named *Megavirus chilensis*, it can be seen with a basic optical microscope.[52] In 2013, the Pandoravirus genus was discovered in Chile and Australia, and has genomes about twice as large as Megavirus and Mimivirus.[53] All giant viruses have dsDNA genomes and they are classified into several families: *Mimiviridae, Pithoviridae, Pandoraviridae, Phycodnaviridae*, and the Mollivirus genus.[54]

Some viruses that infect Archaea have complex structures unrelated to any other form of virus, with a wide variety of unusual shapes, ranging from spindle-shaped structures to viruses that resemble hooked rods, teardrops or even bottles. Other archaeal viruses resemble the tailed bacteriophages, and can have multiple tail structures.[55]

Genome

Genomic diversity among viruses

Property	Parameters
Nucleic acid	• DNA • RNA

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	• Both DNA and RNA (at different stages in the life cycle)
Shape	• Linear • Circular • Segmented
Strandedness	• Single-stranded (ss) • Double-stranded (ds) • Double-stranded with regions of single-strandedness
Sense	• Positive sense (+) • Negative sense (−) • Ambisense (+/−)

An enormous variety of genomic structures can be seen among viral species; as a group, they contain more structural genomic diversity than plants, animals, archaea, or bacteria. There are millions of different types of viruses,[8] although fewer than 7,000 types have been described in detail.[6]:49 As of January 2021, the NCBI Virus genome database has more than 193,000 complete genome sequences,[56] but there are doubtlessly many more to be discovered.[57][58]

A virus has either a DNA or an RNA genome and is called a DNA virus or an RNA virus, respectively. Most viruses have RNA genomes. Plant viruses tend to have single-stranded RNA genomes and bacteriophages tend to have double-stranded DNA genomes.[26]:96–99

Viral genomes are circular, as in the polyomaviruses, or linear, as in the adenoviruses. The type of nucleic acid is irrelevant to the shape of the genome. Among RNA viruses and certain DNA viruses, the genome is often divided into separate parts, in which case it is called segmented. For RNA viruses, each segment often codes for only one protein and they are usually found together in one capsid. All segments are not required to be in the same virion for the virus to be infectious, as demonstrated by brome mosaic virus and several other plant viruses.[26]:33–35

A viral genome, irrespective of nucleic acid type, is almost always either single-stranded (ss) or double-stranded (ds). Single-stranded genomes consist of an unpaired nucleic acid, analogous to one-half of a ladder split down the middle. Double-stranded genomes consist of two complementary paired nucleic acids, analogous to a ladder. The virus particles of some virus families, such as

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those belonging to the *Hepadnaviridae*, contain a genome that is partially double-stranded and partially single-stranded.[26]: 96–99

For most viruses with RNA genomes and some with single-stranded DNA (ssDNA) genomes, the single strands are said to be either positive-sense (called the 'plus-strand') or negative-sense (called the 'minus-strand'), depending on if they are complementary to the viral messenger RNA (mRNA). Positive-sense viral RNA is in the same sense as viral mRNA and thus at least a part of it can be immediately translated by the host cell. Negative-sense viral RNA is complementary to mRNA and thus must be converted to positive-sense RNA by an RNA-dependent RNA polymerase before translation. DNA nomenclature for viruses with genomic ssDNA is similar to RNA nomenclature, in that positive-strand viral ssDNA is identical in sequence to the viral mRNA and is thus a coding strand, while negative-sense viral ssDNA is complementary to the viral mRNA and is thus a template strand.[26]: 96–99 Several types of ssDNA and ssRNA viruses have genomes that are ambisense in that transcription can occur off both strands in a double-stranded replicative intermediate. Examples include geminiviruses, which are ssDNA plant viruses and arenaviruses, which are ssRNA viruses of animals.[59]

Genome size

Genome size varies greatly between species. The smallest—the ssDNA circoviruses, family *Circoviridae*—code for only two proteins and have a genome size of only two kilobases;[60] the largest—the pandoraviruses—have genome sizes of around two megabases which code for about 2500 proteins.[53] Virus genes rarely have introns and often are arranged in the genome so that they overlap.[61]

In general, RNA viruses have smaller genome sizes than DNA viruses because of a higher error-rate when replicating, and have a maximum upper size limit.[24] Beyond this, errors when replicating render the virus useless or uncompetitive. To compensate, RNA viruses often have segmented genomes—the genome is split into smaller molecules—thus reducing the chance that an error in a single-component genome will incapacitate the entire genome. In contrast, DNA viruses generally have larger genomes because of the high fidelity of their replication enzymes.[62] Single-strand DNA viruses are an

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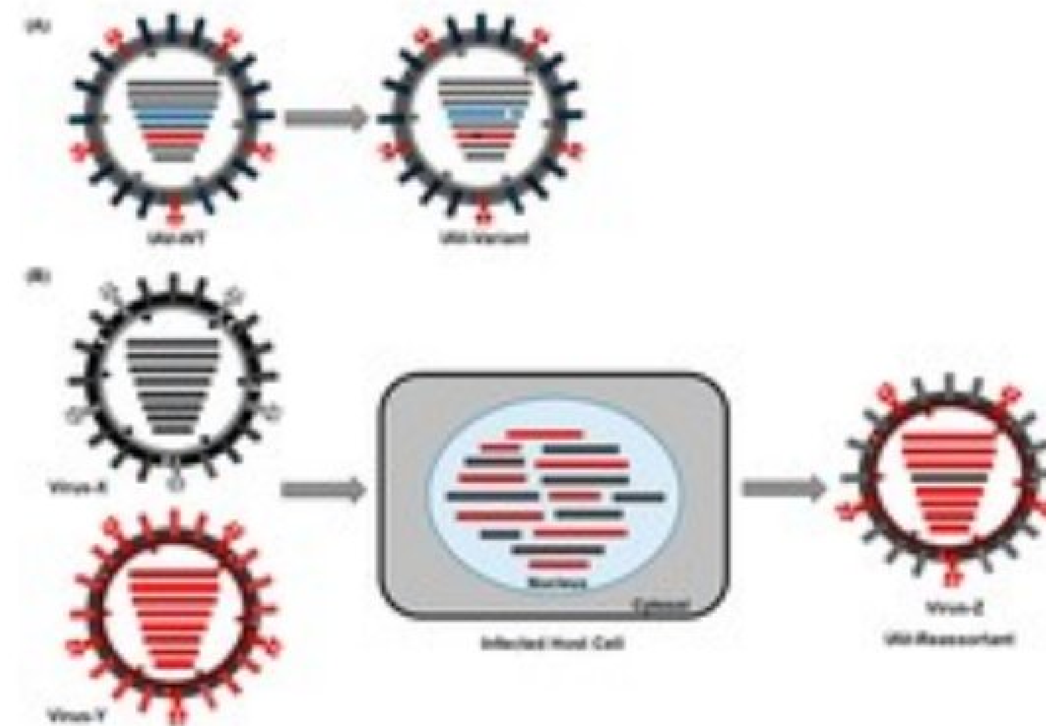
exception to this rule, as mutation rates for these genomes can approach the extreme of the ssRNA virus case.[63]

Genetic mutation and recombination



Evolution mechanisms of Influenza A virus. (A) **Antigenic Drift**: Gradual accumulation of mutations in the genome of IAVs leads to emergence of new virus variants. (B) **Antigenic Shift**: The reassortment of genetic segments between two or more invading IAVs in a host cell can lead to emergence of an antigenically novel subtype.

Viruses undergo genetic change by several mechanisms. These include a process called antigenic drift where individual bases in the DNA or RNA mutate to other bases. Most of these point mutations are "silent"—they do not change the protein that the gene encodes—but others can confer evolutionary advantages such as resistance to antiviral drugs.[64][65] Antigenic shift occurs when there is a major change in the genome of the virus. This can be a result of recombination or reassortment. The Influenza A virus is highly prone to reassortment; occasionally this has resulted in novel strains which have caused pandemics.[66] RNA viruses often exist as quasispecies or swarms of viruses of the same species but with slightly different genome nucleoside sequences. Such quasispecies are a prime target for natural selection.[67]

Segmented genomes confer evolutionary advantages; different strains of a virus with a segmented genome can shuffle and combine genes and produce progeny viruses (or offspring) that have unique characteristics. This is called reassortment or 'viral sex'.[68]

Genetic recombination is a process by which a strand of DNA (or RNA) is broken and then joined to the end of a different DNA (or RNA) molecule. This can occur when viruses infect cells simultaneously and studies of viral evolution have shown that recombination has been rampant in the species studied.[69] Recombination is common to both RNA and DNA viruses.[70][71]

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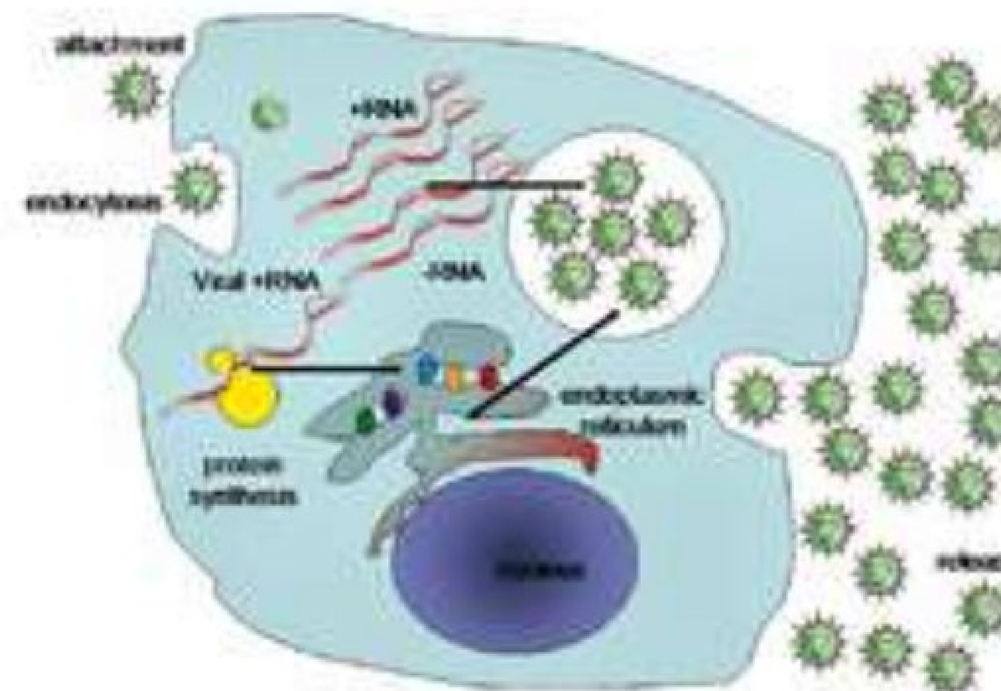
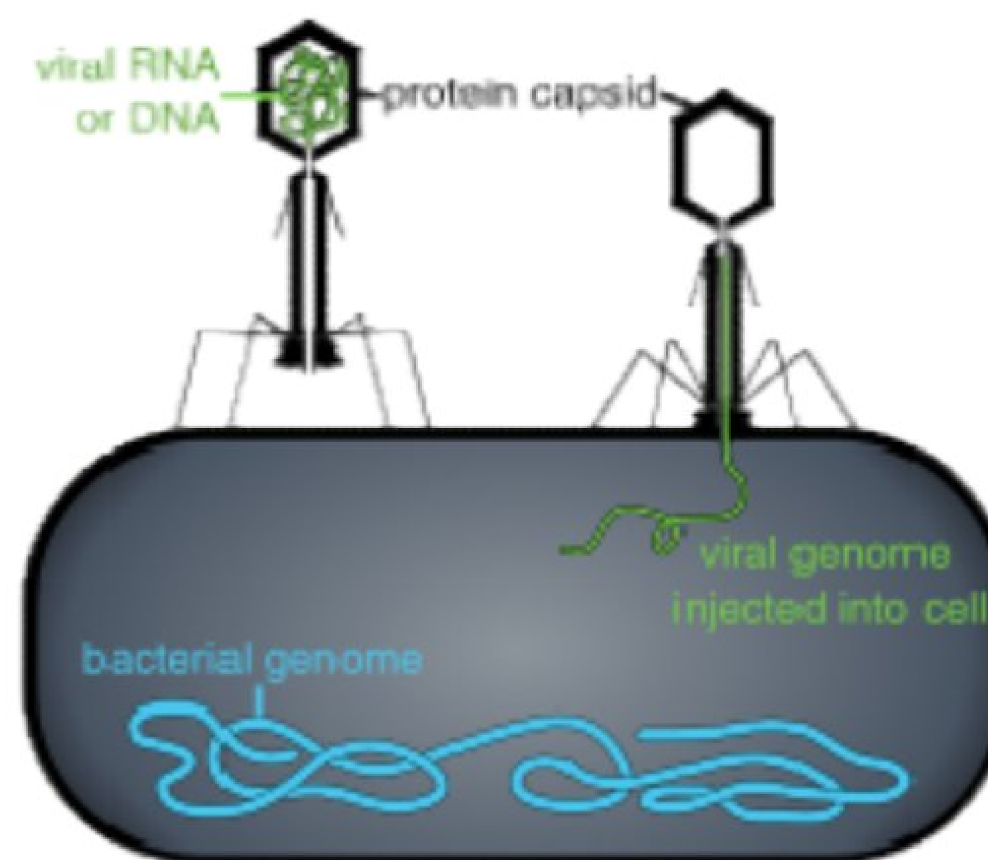
Coronaviruses have a single-strand positive-sense RNA genome. Replication of the genome is catalyzed by an RNA-dependent RNA polymerase. The mechanism of recombination used by coronaviruses likely involves template switching by the polymerase during genome replication.[72] This process appears to be an adaptation for coping with genome damage.[73]

Replication cycle



A typical virus replication cycle



Some bacteriophages inject their genomes into bacterial cells (not to scale)

Viral populations do not grow through cell division, because they are acellular. Instead, they use the machinery and metabolism of a host cell to produce multiple copies of themselves, and they assemble in the cell.[74] When infected, the host cell is forced to rapidly produce thousands of copies of the original virus.[75]

Their life cycle differs greatly between species, but there are six basic stages in their life cycle:[26]:75–91

Attachment is a specific binding between viral capsid proteins and specific receptors on the host cellular surface. This specificity determines the host range and type of host cell of a virus. For example, HIV infects a limited range of human leucocytes. This is because its surface protein, gp120, specifically interacts with the CD4 molecule—a chemokine receptor—which is most commonly found on the surface of CD4+ T-Cells. This

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mechanism has evolved to favour those viruses that infect only cells in which they are capable of replication. Attachment to the receptor can induce the viral envelope protein to undergo changes that result in the fusion of viral and cellular membranes, or changes of non-enveloped virus surface proteins that allow the virus to enter.[76]

Penetration or *viral entry* follows attachment: Virions enter the host cell through receptor-mediated endocytosis or membrane fusion. The infection of plant and fungal cells is different from that of animal cells. Plants have a rigid cell wall made of cellulose, and fungi one of chitin, so most viruses can get inside these cells only after trauma to the cell wall.[6]:70 Nearly all plant viruses (such as tobacco mosaic virus) can also move directly from cell to cell, in the form of single-stranded nucleoprotein complexes, through pores called plasmodesmata.[77] Bacteria, like plants, have strong cell walls that a virus must breach to infect the cell. Given that bacterial cell walls are much thinner than plant cell walls due to their much smaller size, some viruses have evolved mechanisms that inject their genome into the bacterial cell across the cell wall, while the viral capsid remains outside.[6]:71

Uncoating is a process in which the viral capsid is removed: This may be by degradation by viral enzymes or host enzymes or by simple dissociation; the end-result is the releasing of the viral genomic nucleic acid.[78]

Replication of viruses involves primarily multiplication of the genome. Replication involves the synthesis of viral messenger RNA (mRNA) from "early" genes (with exceptions for positive-sense RNA viruses), viral protein synthesis, possible assembly of viral proteins, then viral genome replication mediated by early or regulatory protein expression. This may be followed, for complex viruses with larger genomes, by one or more further rounds of mRNA synthesis: "late" gene expression is, in general, of structural or virion proteins.[79]

Assembly – Following the structure-mediated self-assembly of the virus particles, some modification of the proteins often occurs. In viruses such as HIV, this modification (sometimes called maturation) occurs after the virus has been released from the host cell.[80]

Release – Viruses can be released from the host cell by lysis, a process that kills the cell by bursting its

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membrane and cell wall if present: this is a feature of many bacterial and some animal viruses. Some viruses undergo a lysogenic cycle where the viral genome is incorporated by genetic recombination into a specific place in the host's chromosome. The viral genome is then known as a "provirus" or, in the case of bacteriophages a "prophage".[13]:836 Whenever the host divides, the viral genome is also replicated. The viral genome is mostly silent within the host. At some point, the provirus or prophage may give rise to the active virus, which may lyse the host cells.[6]:243–259 Enveloped viruses (e.g., HIV) typically are released from the host cell by budding. During this process, the virus acquires its envelope, which is a modified piece of the host's plasma or other, internal membrane.[6]:185–187

Genome replication

The genetic material within virus particles, and the method by which the material is replicated, varies considerably between different types of viruses.

DNA viruses

The genome replication of most DNA viruses takes place in the cell's nucleus. If the cell has the appropriate receptor on its surface, these viruses enter the cell either by direct fusion with the cell membrane (e.g., herpesviruses) or—more usually—by receptor-mediated endocytosis. Most DNA viruses are entirely dependent on the host cell's DNA and RNA synthesising machinery and RNA processing machinery. Viruses with larger genomes may encode much of this machinery themselves. In eukaryotes, the viral genome must cross the cell's nuclear membrane to access this machinery, while in bacteria it need only enter the cell.[13]:118[26]:78

RNA viruses

Replication of RNA viruses usually takes place in the cytoplasm. RNA viruses can be placed into four different groups depending on their modes of replication. The polarity (whether or not it can be used directly by ribosomes to make proteins) of single-stranded RNA viruses largely determines the replicative mechanism; the other major criterion is whether the genetic material is single-stranded or double-stranded. All RNA viruses use their own RNA replicase enzymes to create copies of their genomes.[26]:79

Reverse transcribing viruses

Reverse transcribing viruses have ssRNA (*Retroviridae*, *Metaviridae*, *Pseudoviridae*) or dsDNA (*Caulimoviridae*, and *Hepadnaviridae*) in their particles. Reverse transcribing viruses with RNA genomes (retroviruses) use a DNA intermediate to replicate, whereas those with DNA genomes (pararetroviruses) use an RNA intermediate during genome replication. Both types use a reverse transcriptase, or RNA-dependent DNA polymerase enzyme, to carry out the nucleic acid conversion. Retroviruses

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integrate the DNA produced by reverse transcription into the host genome as a provirus as a part of the replication process; pararetroviruses do not, although integrated genome copies of especially plant pararetroviruses can give rise to infectious virus.[81] They are susceptible to antiviral drugs that inhibit the reverse transcriptase enzyme, e.g. zidovudine and lamivudine. An example of the first type is HIV, which is a retrovirus. Examples of the second type are the *Hepadnaviridae*, which includes Hepatitis B virus.[26]:88–89

Cytopathic effects on the host cell

The range of structural and biochemical effects that viruses have on the host cell is extensive.[26]:115–146 These are called 'cytopathic effects'.[26]:115 Most virus infections eventually result in the death of the host cell. The causes of death include cell lysis, alterations to the cell's surface membrane and apoptosis.[82] Often cell death is caused by cessation of its normal activities because of suppression by virus-specific proteins, not all of which are components of the virus particle.[83] The distinction between cytopathic and harmless is gradual. Some viruses, such as Epstein–Barr virus, can cause cells to proliferate without causing malignancy,[84] while others, such as papillomaviruses, are established causes of cancer.[85]

Dormant and latent infections

Some viruses cause no apparent changes to the infected cell. Cells in which the virus is latent and inactive show few signs of infection and often function normally.[86] This causes persistent infections and the virus is often dormant for many months or years. This is often the case with herpes viruses.[87][88]

Host range

Viruses are by far the most abundant biological entities on Earth and they outnumber all the others put together.[89] They infect all types of cellular life including animals, plants, bacteria and fungi.[6]:49 Different types of viruses can infect only a limited range of hosts and many are species-specific. Some, such as smallpox virus for example, can infect only one species—in this case humans,[13]:643 and are said to have a narrow host range. Other viruses, such as rabies virus, can infect different species

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of mammals and are said to have a broad range.[13]:631 The viruses that infect plants are harmless to animals, and most viruses that infect other animals are harmless to humans.[6]:272 The host range of some bacteriophages is limited to a single strain of bacteria and they can be used to trace the source of outbreaks of infections by a method called phage typing.[90] The complete set of viruses in an organism or habitat is called the virome; for example, all human viruses constitute the human virome.[91]

Novel viruses

A **novel virus** is one that has not previously been recorded. It can be a virus that is isolated from its natural reservoir or isolated as the result of spread to an animal or human host where the virus had not been identified before. It can be an emergent virus, one that represents a new virus, but it can also be an extant virus that has not been previously identified.[92] The SARS-CoV-2 coronavirus that caused the COVID-19 pandemic is an example of a novel virus.[93]

Classification

Main article: Virus classification

Classification seeks to describe the diversity of viruses by naming and grouping them on the basis of similarities. In 1962, André Lwoff, Robert Horne, and Paul Tournier were the first to develop a means of virus classification, based on the Linnaean hierarchical system.[94] This system based classification on phylum, class, order, family, genus, and species. Viruses were grouped according to their shared properties (not those of their hosts) and the type of nucleic acid forming their genomes.[95] In 1966, the International Committee on Taxonomy of Viruses (ICTV) was formed. The system proposed by Lwoff, Horne and Tournier was initially not accepted by the ICTV because the small genome size of viruses and their high rate of mutation made it difficult to determine their ancestry beyond order. As such, the Baltimore classification system has come to

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be used to supplement the more traditional hierarchy.[96] Starting in 2018, the ICTV began to acknowledge deeper evolutionary relationships between viruses that have been discovered over time and adopted a 15-rank classification system ranging from realm to species.[97] Additionally, some species within the same genus are grouped into a **genogroup**.[98][99]

ICTV classification

The ICTV developed the current classification system and wrote guidelines that put a greater weight on certain virus properties to maintain family uniformity. A unified taxonomy (a universal system for classifying viruses) has been established.[100] Only a small part of the total diversity of viruses has been studied.[101] As of 2022, 6 realms, 10 kingdoms, 17 phyla, 2 subphyla, 40 classes, 72 orders, 8 suborders, 264 families, 182 subfamilies, 2,818 genera, 84 subgenera, and 11,273 species of viruses have been defined by the ICTV.[7]

The general taxonomic structure of taxon ranges and the suffixes used in taxonomic names are shown hereafter. As of 2022, the ranks of subrealm, subkingdom, and subclass are unused, whereas all other ranks are in use.[7]

Realm (-*viria*)

Subrealm (-*vira*)

Kingdom (-*virae*)

Subkingdom (-*virites*)

Phylum (-*viricota*)

Subphylum (-*viricotina*)

Class (-*viricetes*)

Subclass (-*viricetidae*)

Order (-*virales*)

Suborder (-*virineae*)

Family (-*viridae*)

Subfamily (-*virinae*)

Genus (-*virus*)

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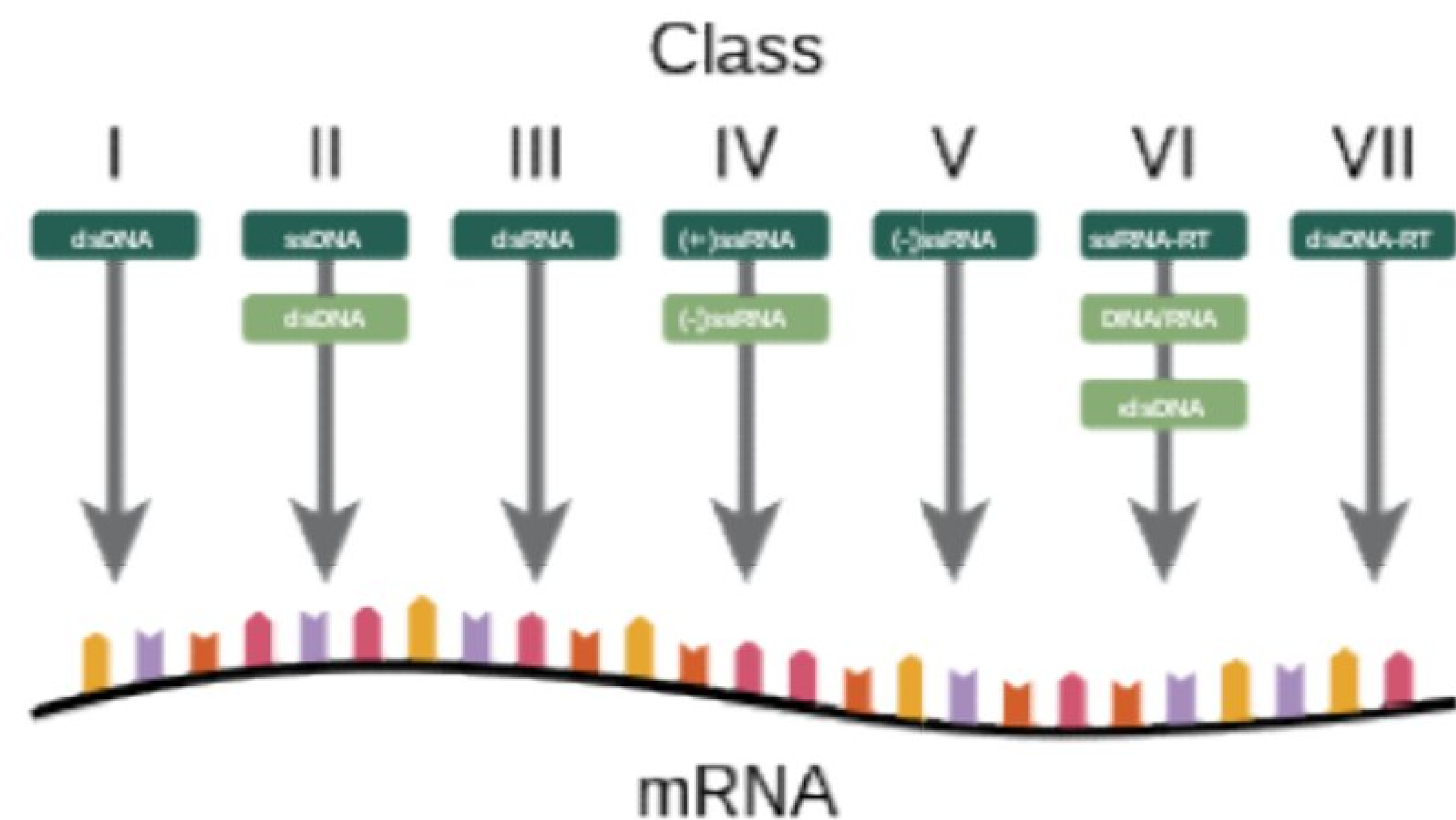
Subgenus (-*virus*)

Species

Baltimore classification

Main article: Baltimore classification



The Baltimore Classification of viruses is based on the method of viral mRNA synthesis

The Nobel Prize-winning biologist David Baltimore devised the Baltimore classification system.[102][103] The ICTV classification system is used in conjunction with the Baltimore classification system in modern virus classification.[104][105][106]

The Baltimore classification of viruses is based on the mechanism of mRNA production. Viruses must generate mRNAs from their genomes to produce proteins and replicate themselves, but different mechanisms are used to achieve this in each virus family. Viral genomes may be single-stranded (ss) or double-stranded (ds), RNA or DNA, and may or may not use reverse transcriptase (RT). In addition, ssRNA viruses may be either sense (+) or antisense (−). This classification places viruses into seven groups:

- I: dsDNA viruses (e.g. Adenoviruses, Herpesviruses, Poxviruses)
- II: ssDNA viruses (+ strand or "sense") DNA (e.g. Parvoviruses)
- III: dsRNA viruses (e.g. Reoviruses)
- IV:(+)ssRNA viruses (+ strand or sense) RNA

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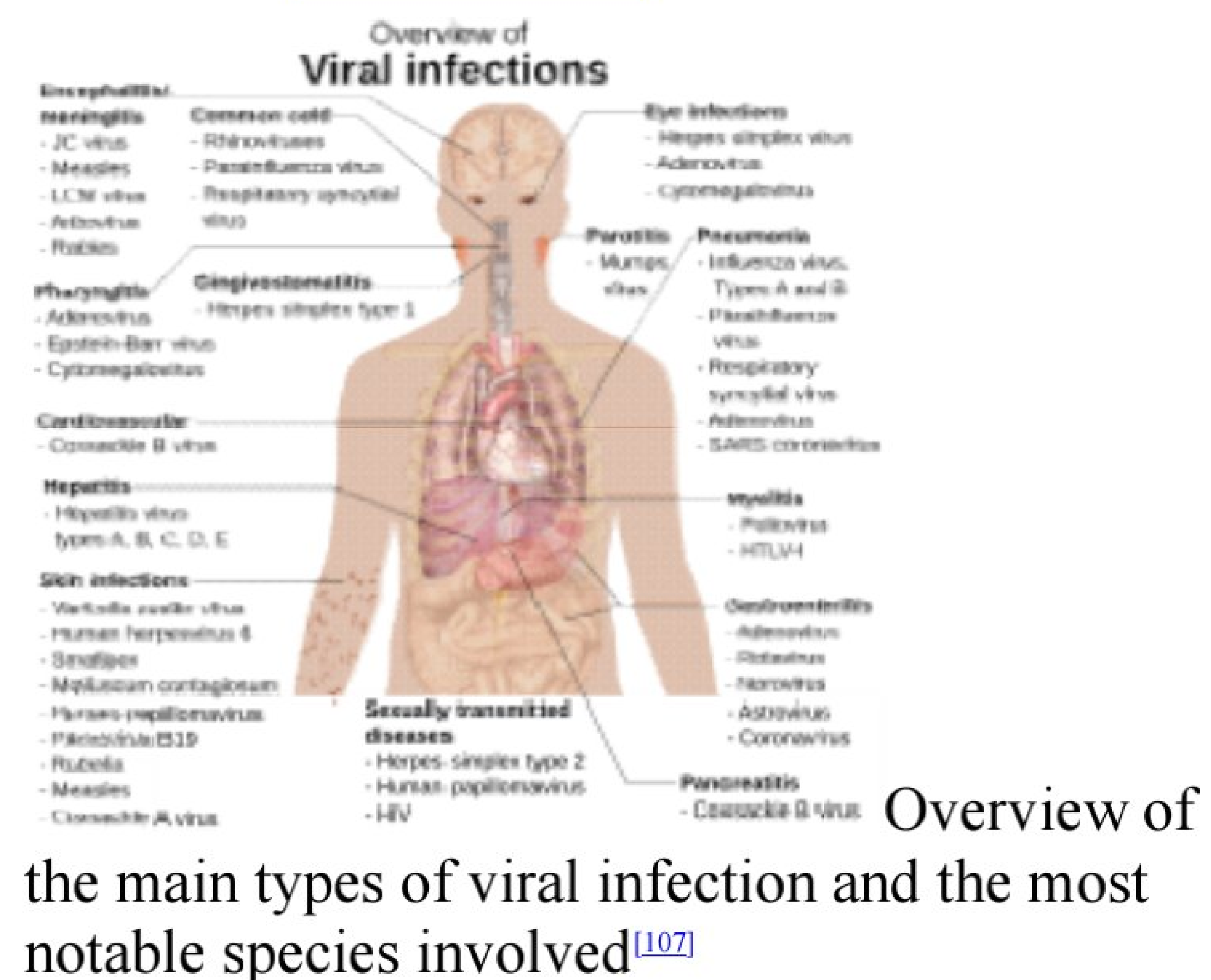
(e.g. Coronaviruses, Picornaviruses, Togaviruses)
- V: (−)ssRNA viruses (− strand or antisense) RNA (e.g. Orthomyxoviruses, Rhabdoviruses)
- VI: ssRNA-RT viruses (+ strand or sense) RNA with DNA intermediate in life-cycle (e.g. Retroviruses)
- VII: dsDNA-RT viruses DNA with RNA intermediate in life-cycle (e.g. Hepadnaviruses)

Role in human disease

See also: Viral disease



Overview of the main types of viral infection and the most notable species involved[107]

Examples of common human diseases caused by viruses include the common cold, influenza, chickenpox, and cold sores. Many serious diseases such as rabies, Ebola virus disease, AIDS (HIV), avian influenza, and SARS are caused by viruses. The relative ability of viruses to cause disease is described in terms of virulence. Other diseases are under investigation to discover if they have a virus as the causative agent, such as the possible connection between human herpesvirus 6 (HHV6) and neurological diseases such as multiple sclerosis and chronic fatigue syndrome.[108] There is controversy over whether the bornavirus, previously thought to cause neurological diseases in horses,

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could be responsible for psychiatric illnesses in humans.[109]

Viruses have different mechanisms by which they produce disease in an organism, which depends largely on the viral species. Mechanisms at the cellular level primarily include cell lysis, the breaking open and subsequent death of the cell. In multicellular organisms, if enough cells die, the whole organism will start to suffer the effects. Although viruses cause disruption of healthy homeostasis, resulting in disease, they may exist relatively harmlessly within an organism. An example would include the ability of the herpes simplex virus, which causes cold sores, to remain in a dormant state within the human body. This is called latency[110] and is a characteristic of the herpes viruses, including Epstein–Barr virus, which causes glandular fever, and varicella zoster virus, which causes chickenpox and shingles. Most people have been infected with at least one of these types of herpes virus.[111] These latent viruses might sometimes be beneficial, as the presence of the virus can increase immunity against bacterial pathogens, such as *Yersinia pestis*.[112]

Some viruses can cause lifelong or chronic infections, where the viruses continue to replicate in the body despite the host's defence mechanisms.[113] This is common in hepatitis B virus and hepatitis C virus infections. People chronically infected are known as carriers, as they serve as reservoirs of infectious virus.[114] In populations with a high proportion of carriers, the disease is said to be endemic.[115]

Bacteria are ubiquitous, mostly free-living organisms often consisting of one biological cell. They constitute a large domain of prokaryotic microorganisms. Typically a few micrometres in length, bacteria were among the first life forms to appear on Earth, and are present in most of its habitats. Bacteria inhabit soil, water, acidic hot springs, radioactive waste, and the deep biosphere of Earth's crust. Bacteria play a vital role in many stages of the nutrient cycle by recycling nutrients and the fixation of

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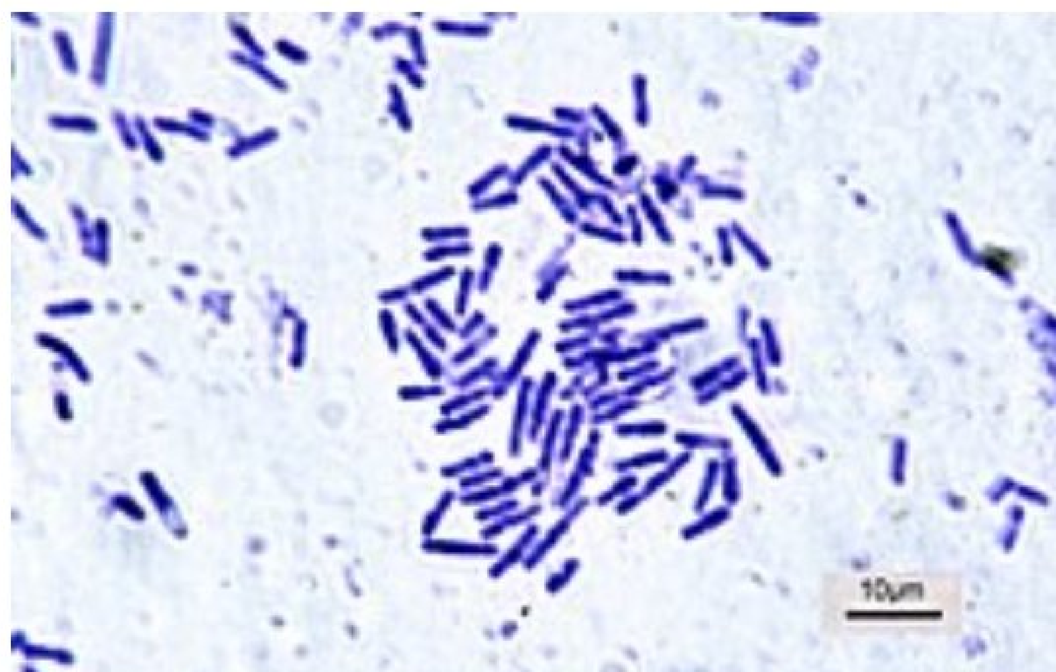
nitrogen from the atmosphere. The nutrient cycle includes the decomposition of dead bodies; bacteria are responsible for the putrefaction stage in this process. In the biological communities surrounding hydrothermal vents and cold seeps, extremophile bacteria provide the nutrients needed to sustain life by converting dissolved compounds, such as hydrogen sulphide and methane, to energy. Bacteria also live in mutualistic, commensal and parasitic relationships with plants and animals. Most bacteria have not been characterised and there are many species that cannot be grown in the laboratory. The study of bacteria is known as bacteriology, a branch of microbiology.

Like all animals, humans carry vast numbers (approximately 10^{13} to 10^{14}) of bacteria.[2] Most are in the gut, though there are many on the skin. Most of the bacteria in and on the body are harmless or rendered so by the protective effects of the immune system, and many are beneficial,[3] particularly the ones in the gut. However, several species of bacteria are pathogenic and cause infectious diseases, including cholera, syphilis, anthrax, leprosy, tuberculosis, tetanus and bubonic plague. The most common fatal bacterial diseases are respiratory infections. Antibiotics are used to treat bacterial infections and are also used in farming, making antibiotic resistance a growing problem. Bacteria are important in sewage treatment and the breakdown of oil spills, the production of cheese and yogurt through fermentation, the recovery of gold, palladium, copper and other metals in the mining sector (biomining, bioleaching), as well as in biotechnology, and the manufacture of antibiotics and other chemicals.

Once regarded as plants constituting the class *Schizomycetes* ("fission fungi"), bacteria are now classified as prokaryotes. Unlike cells of animals and other eukaryotes, bacterial cells do not contain a nucleus and rarely harbour membrane-bound organelles. Although the term *bacteria* traditionally included all prokaryotes, the scientific classification changed after the discovery in the 1990s that prokaryotes consist of two very different groups of organisms that evolved from an ancient common ancestor. These evolutionary domains are called Bacteria and Archaea.[4]

Etymology



Rod-shaped *Bacillus subtilis*

The word *bacteria* is the plural of the Neo-Latin ***bacterium***, which is the Latinisation of the Ancient Greek βακτήριον (*baktḗrion*),[5] the diminutive of βακτηρία (*baktēría*), meaning "staff, cane",[6] because the first ones to be discovered were rod-shaped.[7][8]

Origin and early evolution

Main article: Evolution of bacteria

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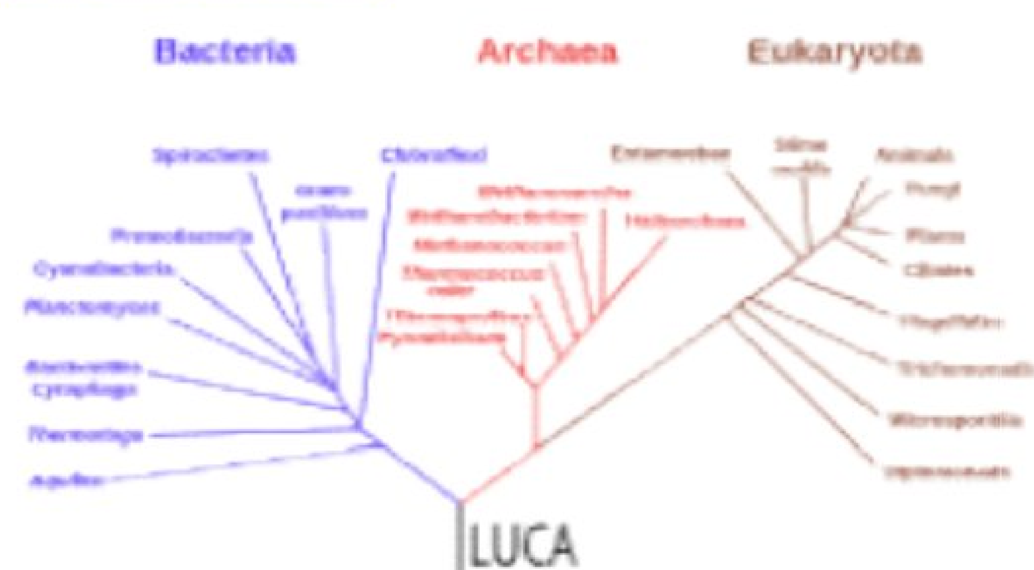
Further information: Earliest known life forms, Evolutionary history of life, and Timeline of evolution



Phylogenetic tree of Bacteria, Archaea and Eukarya, with the last universal common ancestor (LUCA) at the root.[9]

The ancestors of bacteria were unicellular microorganisms that were the first forms of life to appear on Earth, about 4 billion years ago.[10] For about 3 billion years, most organisms were microscopic, and bacteria and archaea were the dominant forms of life.[11][12][13] Although bacterial fossils exist, such as stromatolites, their lack of distinctive morphology prevents them from being used to examine the history of bacterial evolution, or to date the time of origin of a particular bacterial species. However, gene sequences can be used to reconstruct the bacterial phylogeny, and these studies indicate that bacteria diverged first from the archaeal/eukaryotic lineage.[14] The most recent common ancestor (MRCA) of bacteria and archaea was probably a hyperthermophile that lived about 2.5 billion–3.2 billion years ago.[15][16][17] The earliest life on land may have been bacteria some 3.22 billion years ago.[18]

Bacteria were also involved in the second great evolutionary divergence, that of the archaea and eukaryotes.[19][20] Here, eukaryotes resulted from the entering of ancient bacteria into endosymbiotic associations with the ancestors of eukaryotic cells, which were themselves possibly related to the Archaea.[21][22] This involved the engulfment by proto-eukaryotic cells of alphaproteobacterial symbionts to form either mitochondria or hydrogenosomes, which are still found in all known Eukarya (sometimes in highly reduced form, e.g. in ancient "amitochondrial" protozoa). Later, some eukaryotes that already contained mitochondria also engulfed cyanobacteria-like organisms, leading to the formation of chloroplasts in algae and plants. This is known as primary endosymbiosis.[23]

Habitat

Bacteria are ubiquitous, living in every possible habitat on the planet including soil, underwater, deep in Earth's crust and even such extreme environments as acidic hot springs and radioactive waste.[24][25] There are thought to be approximately $2×10^{30}$ bacteria on Earth,[26] forming a biomass that is only exceeded by plants.[27] They are abundant in lakes and oceans, in arctic ice, and geothermal springs[28] where they provide the nutrients needed to sustain life by converting dissolved compounds, such as hydrogen sulphide and methane, to energy.[29] They live on and in plants and animals. Most do not cause diseases, are beneficial to their environments, and are essential for life.[3][30] The soil is a rich source of bacteria and a few grams contain around a thousand million of them. They are all essential to soil ecology, breaking down toxic waste and recycling nutrients. They are even found in the atmosphere and one cubic metre of air holds around one hundred million bacterial cells. The oceans and seas

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harbour around 3 x 10^{26} bacteria which provide up to 50% of the oxygen humans breathe.[31] Only around 2% of bacterial species have been fully studied.[32]

Extremophile bacteria

Habitat	Species	Reference
Cold (minus 15 °C Antarctica)	Cryptoendoliths	[33]
Hot (70–100 °C geysers)	*Thermus aquaticus*	[32]
Radiation, 5MRad	*Deinococcus radiodurans*	[33]
Saline, 47% salt (Dead Sea, Great Salt Lake)	several species	[32][33]
Acid pH 3	several species	[24]
Alkaline pH 12.8	betaproteobacteria	[33]
Space (6 years on a NASA satellite)	*Bacillus subtilis*	[33]
3.2 km underground	several species	[33]
High pressure (Mariana Trench – 1200 atm)	Moritella, Shewanella and others	[33]

Morphology

Further information: Bacterial cell structure § Cell morphology, and Bacterial cellular morphologies

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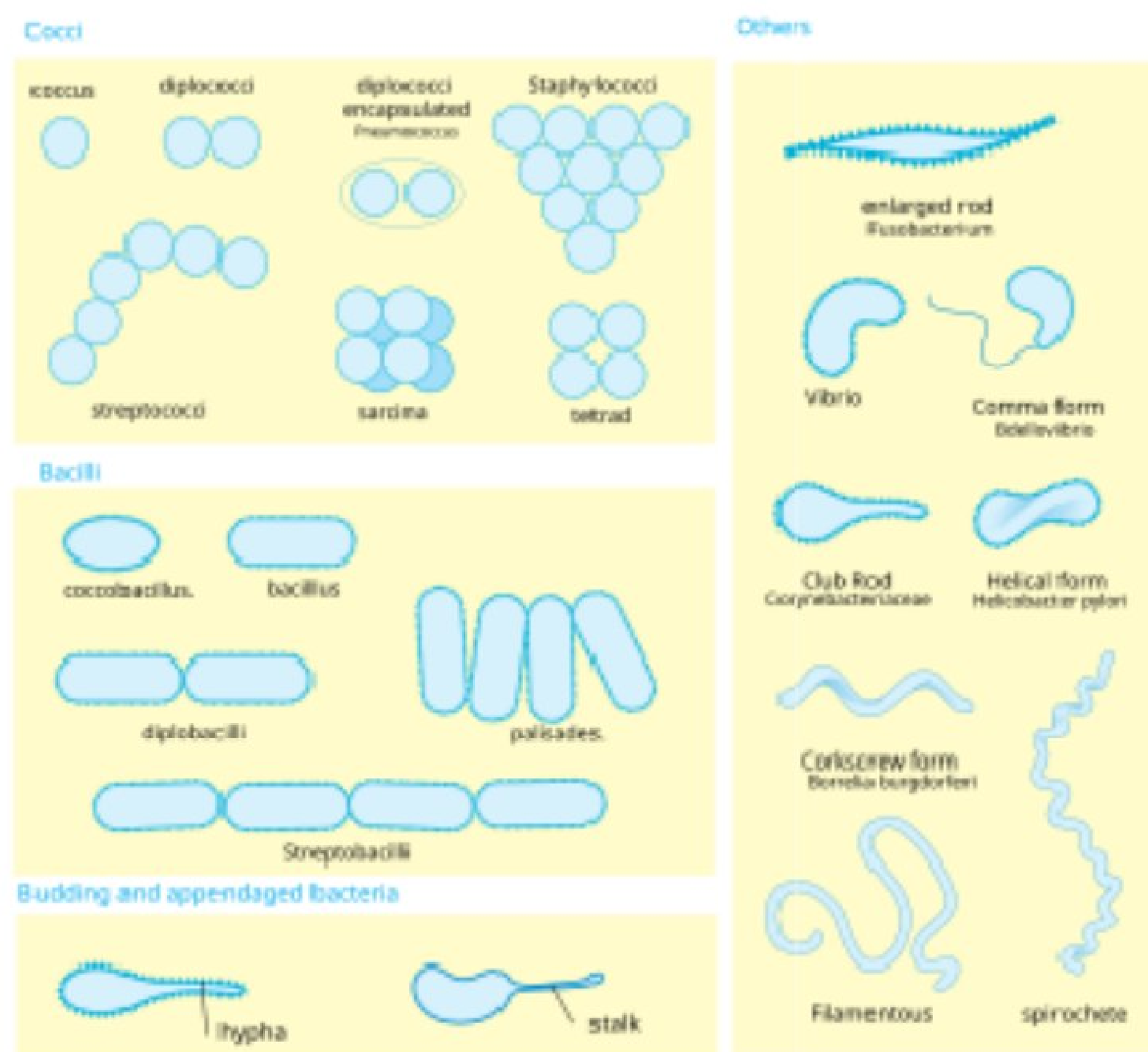
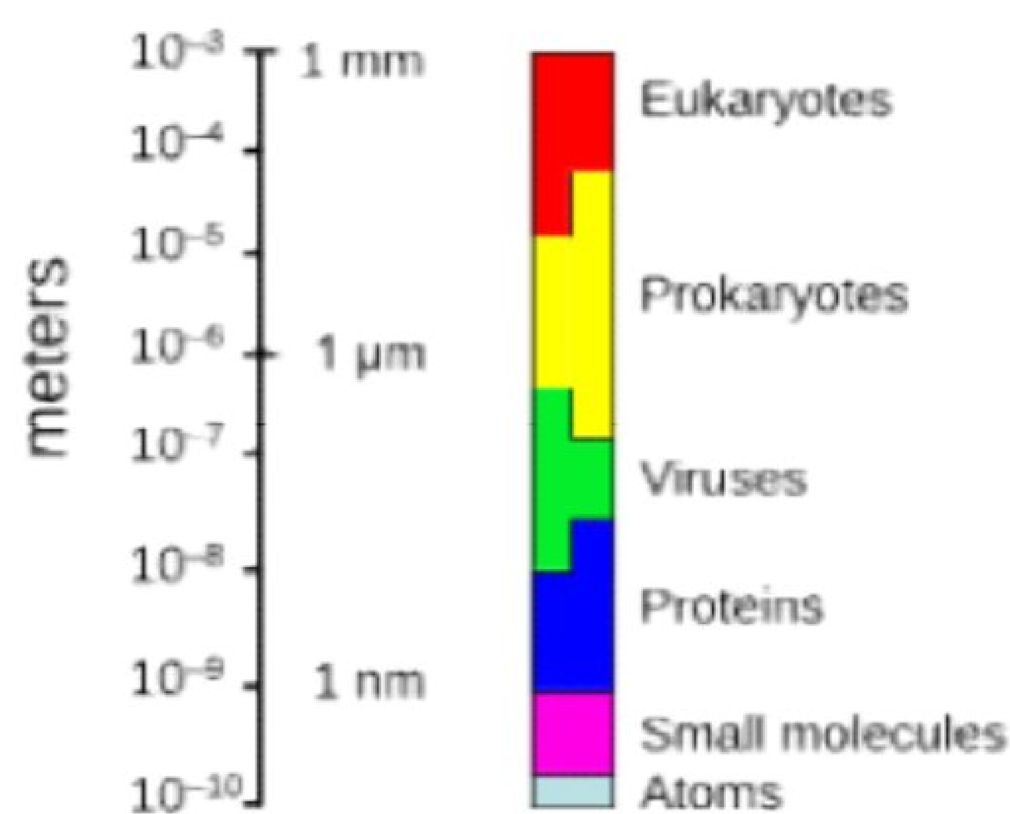


Bacteria display many cell morphologies and arrangements[8]

Size. Bacteria display a wide diversity of shapes and sizes. Bacterial cells are about one-tenth the size of eukaryotic cells and are typically 0.5–5.0 micrometres in length. However, a few species are visible to the unaided eye—for example, *Thiomargarita namibiensis* is up to half a millimetre long,[34] *Epulopiscium fishelsoni* reaches 0.7 mm,[35] and *Thiomargarita magnifica* can reach even 2 cm in length, which is 50 times larger than other known bacteria.[36][37] Among the smallest bacteria are members of the genus *Mycoplasma*, which measure only 0.3 micrometres, as small as the largest viruses.[38] Some bacteria may be even smaller, but these ultramicrobacteria are not well-studied.[39]

Shape. Most bacterial species are either spherical, called *cocci* (*singular coccus*, from Greek *kókkos*, grain, seed), or rod-shaped, called *bacilli* (*sing*. bacillus, from Latin *baculus*, stick).[40] Some bacteria, called *vibrio*, are shaped like slightly curved rods or comma-shaped; others can be spiral-shaped, called *spirilla*, or tightly coiled, called *spirochaetes*. A small number of other unusual shapes have been described, such as star-shaped bacteria.[41] This wide variety of shapes is determined by the bacterial cell wall and cytoskeleton and is important because it can influence the ability of bacteria to acquire nutrients, attach to surfaces, swim through liquids and escape predators.[42][43]



The range of sizes shown by prokaryotes (Bacteria), relative to those of other organisms and biomolecules.[44]

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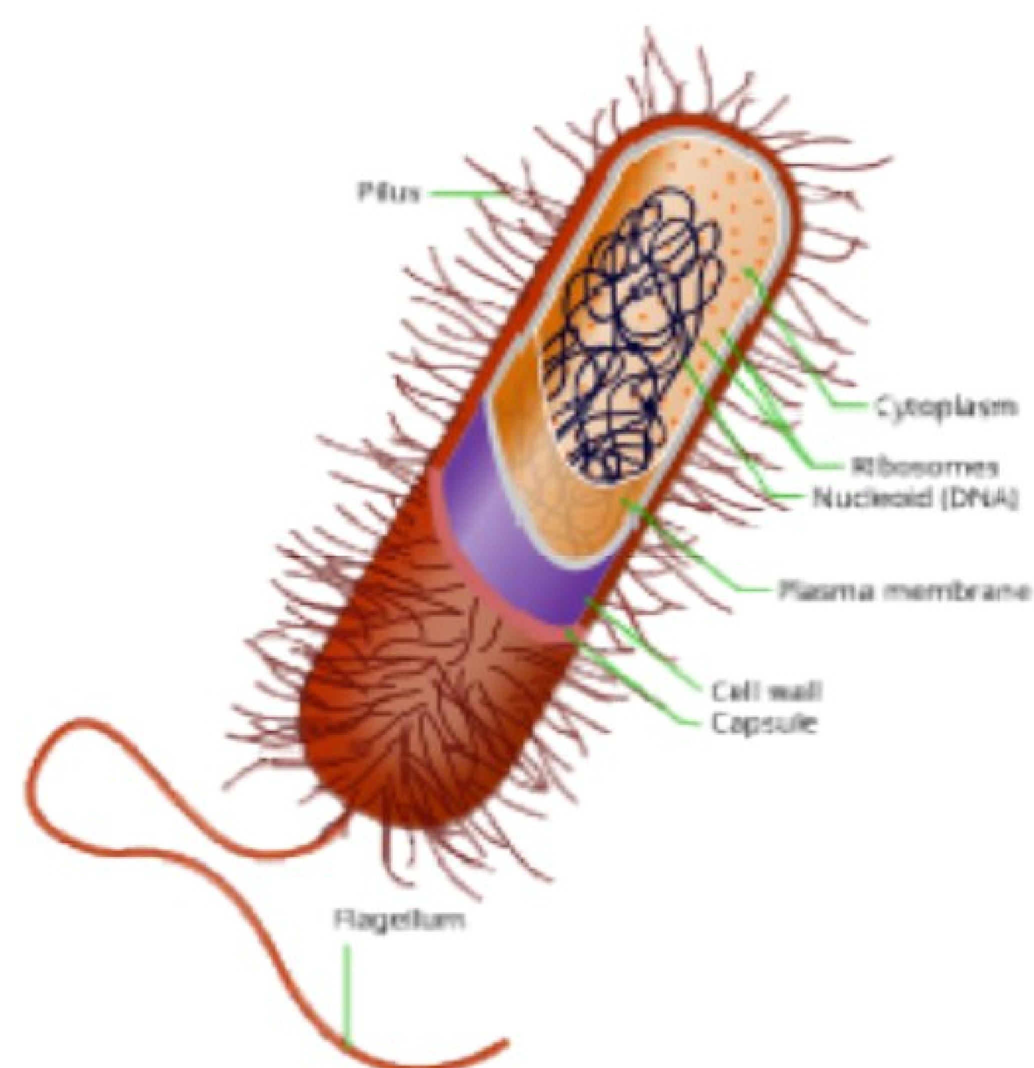
Multicellularity. Most bacterial species exist as single cells; others associate in characteristic patterns: *Neisseria* forms diploids (pairs), streptococci form chains, and staphylococci group together in "bunch of grapes" clusters. Bacteria can also group to form larger multicellular structures, such as the elongated filaments of *Actinomycetota* species, the aggregates of *Myxobacteria* species, and the complex hyphae of *Streptomyces* species.[45] These multicellular structures are often only seen in certain conditions. For example, when starved of amino acids, myxobacteria detect surrounding cells in a process known as quorum sensing, migrate towards each other, and aggregate to form fruiting bodies up to 500 micrometres long and containing approximately 100,000 bacterial cells.[46] In these fruiting bodies, the bacteria perform separate tasks; for example, about one in ten cells migrate to the top of a fruiting body and differentiate into a specialised dormant state called a myxospore, which is more resistant to drying and other adverse environmental conditions.[47]

Biofilms. Bacteria often attach to surfaces and form dense aggregations called biofilms[48] and larger formations known as microbial mats.[49] These biofilms and mats can range from a few micrometres in thickness to up to half a metre in depth, and may contain multiple species of bacteria, protists and archaea. Bacteria living in biofilms display a complex arrangement of cells and extracellular components, forming secondary structures, such as microcolonies, through which there are networks of channels to enable better diffusion of nutrients.[50][51] In natural environments, such as soil or the surfaces of plants, the majority of bacteria are bound to surfaces in biofilms.[52] Biofilms are also important in medicine, as these structures are often present during chronic bacterial infections or in infections of implanted medical devices, and bacteria protected within biofilms are much harder to kill than individual isolated bacteria.[53]

Cellular structure

Further information: Bacterial cell structure



Structure and contents of a typical Gram-positive bacterial cell (seen by the fact that only *one* cell membrane is present).

Intracellular structures

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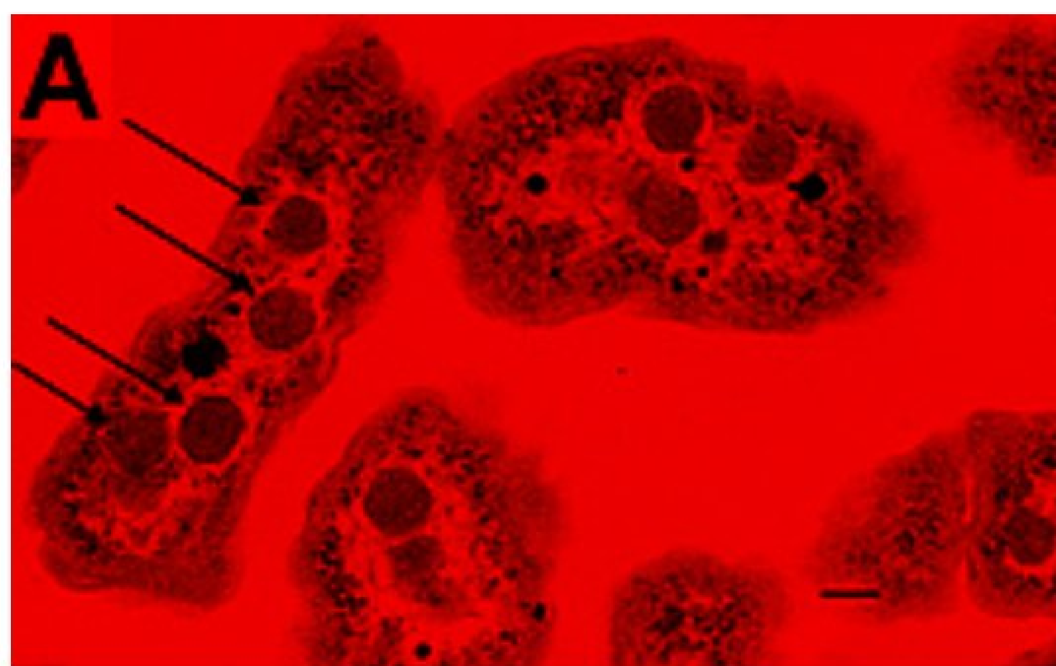
The bacterial cell is surrounded by a cell membrane, which is made primarily of phospholipids. This membrane encloses the contents of the cell and acts as a barrier to hold nutrients, proteins and other essential components of the cytoplasm within the cell.[54] Unlike eukaryotic cells, bacteria usually lack large membrane-bound structures in their cytoplasm such as a nucleus, mitochondria, chloroplasts and the other organelles present in eukaryotic cells.[55] However, some bacteria have protein-bound organelles in the cytoplasm which compartmentalise aspects of bacterial metabolism,[56][57] such as the carboxysome.[58] Additionally, bacteria have a multi-component cytoskeleton to control the localisation of proteins and nucleic acids within the cell, and to manage the process of cell division.[59][60][61]

Many important biochemical reactions, such as energy generation, occur due to concentration gradients across membranes, creating a potential difference analogous to a battery. The general lack of internal membranes in bacteria means these reactions, such as electron transport, occur across the cell membrane between the cytoplasm and the outside of the cell or periplasm.[62] However, in many photosynthetic bacteria, the plasma membrane is highly folded and fills most of the cell with layers of light-gathering membrane.[63] These light-gathering complexes may even form lipid-enclosed structures called chlorosomes in green sulfur bacteria.[64]



An electron micrograph of *Halothiobacillus neapolitanus* cells with carboxysomes inside, with arrows highlighting visible carboxysomes. Scale bars indicate 100 nm.

Bacteria do not have a membrane-bound nucleus, and their genetic material is typically a single circular bacterial chromosome of DNA located in the cytoplasm in an irregularly shaped body called the nucleoid.[65] The nucleoid contains the chromosome with its associated proteins and RNA. Like all other organisms, bacteria contain ribosomes for the production of proteins, but the structure of the bacterial ribosome is different from that of eukaryotes and archaea.[66]

Some bacteria produce intracellular nutrient storage granules, such as glycogen,[67] polyphosphate,[68] sulfur[69] or polyhydroxyalkanoates.[70] Bacteria such as the photosynthetic cyanobacteria, produce internal gas vacuoles, which they use to regulate their buoyancy, allowing them to move up or down into water layers with different light intensities and nutrient levels.[71]

Extracellular structures

Further information: Cell envelope

Around the outside of the cell membrane is the cell wall. Bacterial cell walls are made of peptidoglycan (also called murein), which is made from polysaccharide chains cross-linked by peptides containing D-amino acids.[72] Bacterial cell walls are different from the

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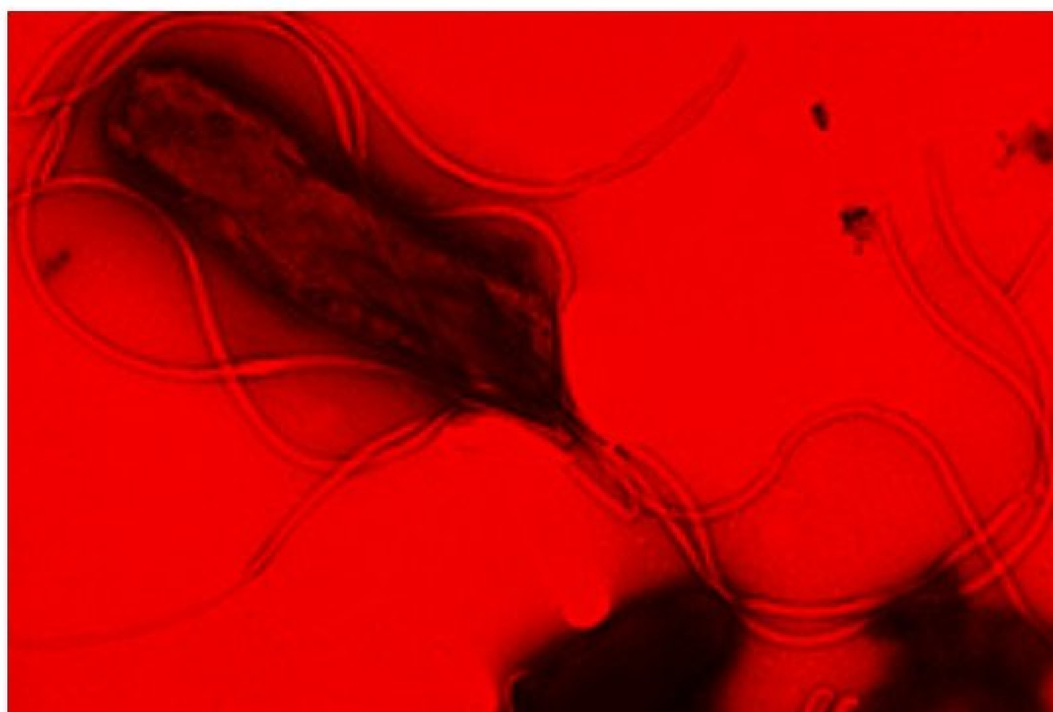
cell walls of plants and fungi, which are made of cellulose and chitin, respectively.[73] The cell wall of bacteria is also distinct from that of achaea, which do not contain peptidoglycan. The cell wall is essential to the survival of many bacteria, and the antibiotic penicillin (produced by a fungus called *Penicillium*) is able to kill bacteria by inhibiting a step in the synthesis of peptidoglycan.[73]

There are broadly speaking two different types of cell wall in bacteria, that classify bacteria into Gram-positive bacteria and Gram-negative bacteria. The names originate from the reaction of cells to the Gram stain, a long-standing test for the classification of bacterial species.[74]

Gram-positive bacteria possess a thick cell wall containing many layers of peptidoglycan and teichoic acids. In contrast, Gram-negative bacteria have a relatively thin cell wall consisting of a few layers of peptidoglycan surrounded by a second lipid membrane containing lipopolysaccharides and lipoproteins. Most bacteria have the Gram-negative cell wall, and only members of the *Bacillota* group and actinomycetota (previously known as the low G+C and high G+C Gram-positive bacteria, respectively) have the alternative Gram-positive arrangement.[75] These differences in structure can produce differences in antibiotic susceptibility; for instance, vancomycin can kill only Gram-positive bacteria and is ineffective against Gram-negative pathogens, such as *Haemophilus influenzae* or *Pseudomonas aeruginosa*.[76] Some bacteria have cell wall structures that are neither classically Gram-positive or Gram-negative. This includes clinically important bacteria such as mycobacteria which have a thick peptidoglycan cell wall like a Gram-positive bacterium, but also a second outer layer of lipids.[77]

In many bacteria, an S-layer of rigidly arrayed protein molecules covers the outside of the cell.[78] This layer provides chemical and physical protection for the cell surface and can act as a macromolecular diffusion barrier. S-layers have diverse functions and are known to act as virulence factors in *Campylobacter* species and contain surface enzymes in *Bacillus stearothermophilus*.[79][80]


Helicobacter pylori electron micrograph, showing multiple flagella on the cell surface

Flagella are rigid protein structures, about 20 nanometres in diameter and up to 20 micrometres in length, that are used for motility. Flagella are driven by the energy released by the transfer of ions down an electrochemical gradient across the cell membrane.[81]

Fimbriae (sometimes called "attachment pili") are fine filaments of protein, usually 2–10 nanometres in diameter and up to several micrometres in length. They are

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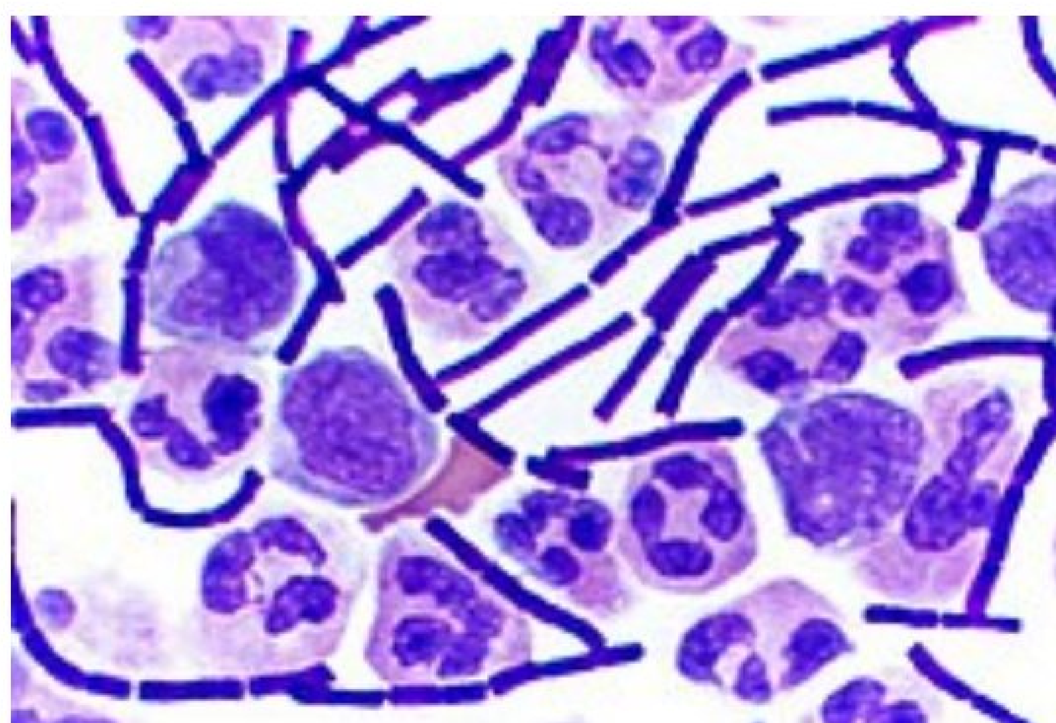
distributed over the surface of the cell, and resemble fine hairs when seen under the electron microscope.[82] Fimbriae are believed to be involved in attachment to solid surfaces or to other cells, and are essential for the virulence of some bacterial pathogens.[83] Pili (*sing*. pilus) are cellular appendages, slightly larger than fimbriae, that can transfer genetic material between bacterial cells in a process called conjugation where they are called conjugation pili or sex pili (see bacterial genetics, below).[84] They can also generate movement where they are called type IV pili.[85]

Glycocalyx is produced by many bacteria to surround their cells,[86] and varies in structural complexity: ranging from a disorganised slime layer of extracellular polymeric substances to a highly structured capsule. These structures can protect cells from engulfment by eukaryotic cells such as macrophages (part of the human immune system).[87] They can also act as antigens and be involved in cell recognition, as well as aiding attachment to surfaces and the formation of biofilms.[88]

The assembly of these extracellular structures is dependent on bacterial secretion systems. These transfer proteins from the cytoplasm into the periplasm or into the environment around the cell. Many types of secretion systems are known and these structures are often essential for the virulence of pathogens, so are intensively studied.[88]

Endospores

Further information: Endospore


Bacillus anthracis (stained purple) growing in cerebrospinal fluid[89]

Some genera of Gram-positive bacteria, such as ***Bacillus***, ***Clostridium***, ***Sporohalobacter***, ***Anaerobacter***, and ***Heliobacterium***, can form highly resistant, dormant structures called ***endospores***.[90] Endospores develop within the cytoplasm of the cell; generally, a single endospore develops in each cell.[91] Each endospore contains a core of DNA and ribosomes surrounded by a cortex layer and protected by a multilayer rigid coat composed of peptidoglycan and a variety of proteins.[91]

Endospores show no detectable metabolism and can survive extreme physical and chemical stresses, such as high levels of UV light, gamma radiation, detergents, disinfectants, heat, freezing, pressure, and desiccation.[92] In this dormant state, these organisms may remain viable for millions of years.[93][94][95] Endospores even allow bacteria to survive exposure to the vacuum and radiation of outer space, leading to the possibility that bacteria could be distributed

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throughout the Universe by space dust, meteoroids, asteroids, comets, planetoids, or directed panspermia.[96][97]

Endospore-forming bacteria can cause disease; for example, anthrax can be contracted by the inhalation of *Bacillus anthracis* endospores, and contamination of deep puncture wounds with *Clostridium tetani* endospores causes tetanus, which, like botulism, is caused by a toxin released by the bacteria that grow from the spores.[98] *Clostridioides difficile* infection, a common problem in healthcare settings, is caused by spore-forming bacteria.[99]

Metabolism

Further information: Microbial metabolism

Bacteria exhibit an extremely wide variety of metabolic types.[100] The distribution of metabolic traits within a group of bacteria has traditionally been used to define their taxonomy, but these traits often do not correspond with modern genetic classifications.[101] Bacterial metabolism is classified into nutritional groups on the basis of three major criteria: the source of energy, the electron donors used, and the source of carbon used for growth.[102]

Phototrophic bacteria derive energy from light using photosynthesis, while chemotrophic bacteria breaking down chemical compounds through oxidation,[103] driving metabolism by transferring electrons from a given electron donor to a terminal electron acceptor in a redox reaction. Chemotrophs are further divided by the types of compounds they use to transfer electrons. Bacteria that derive electrons from inorganic compounds such as hydrogen, carbon monoxide, or ammonia are called lithotrophs, while those that use organic compounds are called organotrophs.[103] Still, more specifically, aerobic organisms use oxygen as the terminal electron acceptor, while anaerobic organisms use other compounds such as nitrate, sulfate, or carbon dioxide.[103]

Many bacteria, called heterotrophs, derive their carbon from other organic carbon. Others, such as cyanobacteria and some purple bacteria, are autotrophic, meaning they obtain cellular carbon by fixing carbon dioxide.[104] In unusual circumstances, the gas methane can be used by methanotrophic bacteria as both a source of electrons and a substrate for carbon anabolism.[105]

Nutritional types in bacterial metabolism

Nutritional type	Source of energy	Source of carbon	Examples
Phototrophs	Sunlight	Organic compounds (photoheterotrophs) or carbon fixation	Cyanobacteria, Green sulfur bacteria, Chloroflexota, or Purple bacteria

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		(photoautotrophs)	
Lithotrophs	Inorganic compounds	Organic compounds (lithoheterotrophs) or carbon fixation (lithoautotrophs)	Thermodesulfobacteriota, Hydrogenophilaceae, or Nitrospirota
Organotrophs	Organic compounds	Organic compounds (chemoheterotrophs) or carbon fixation (chemoautotrophs)	*Bacillus*, *Clostridium*, or Enterobacteriaceae

In many ways, bacterial metabolism provides traits that are useful for ecological stability and for human society. For example, diazotrophs have the ability to fix nitrogen gas using the enzyme nitrogenase.[106] This trait, which can be found in bacteria of most metabolic types listed above,[107] leads to the ecologically important processes of denitrification, sulfate reduction, and acetogenesis, respectively.[108] Bacterial metabolic processes are important drivers in biological responses to pollution; for example, sulfate-reducing bacteria are largely responsible for the production of the highly toxic forms of mercury (methyl- and dimethylmercury) in the environment.[109] Nonrespiratory anaerobes use fermentation to generate energy and reducing power, secreting metabolic by-products (such as ethanol in brewing) as waste. Facultative anaerobes can switch between fermentation and different terminal electron acceptors depending on the environmental conditions in which they find themselves.[110]

Growth and reproduction

Further information: Bacterial growth

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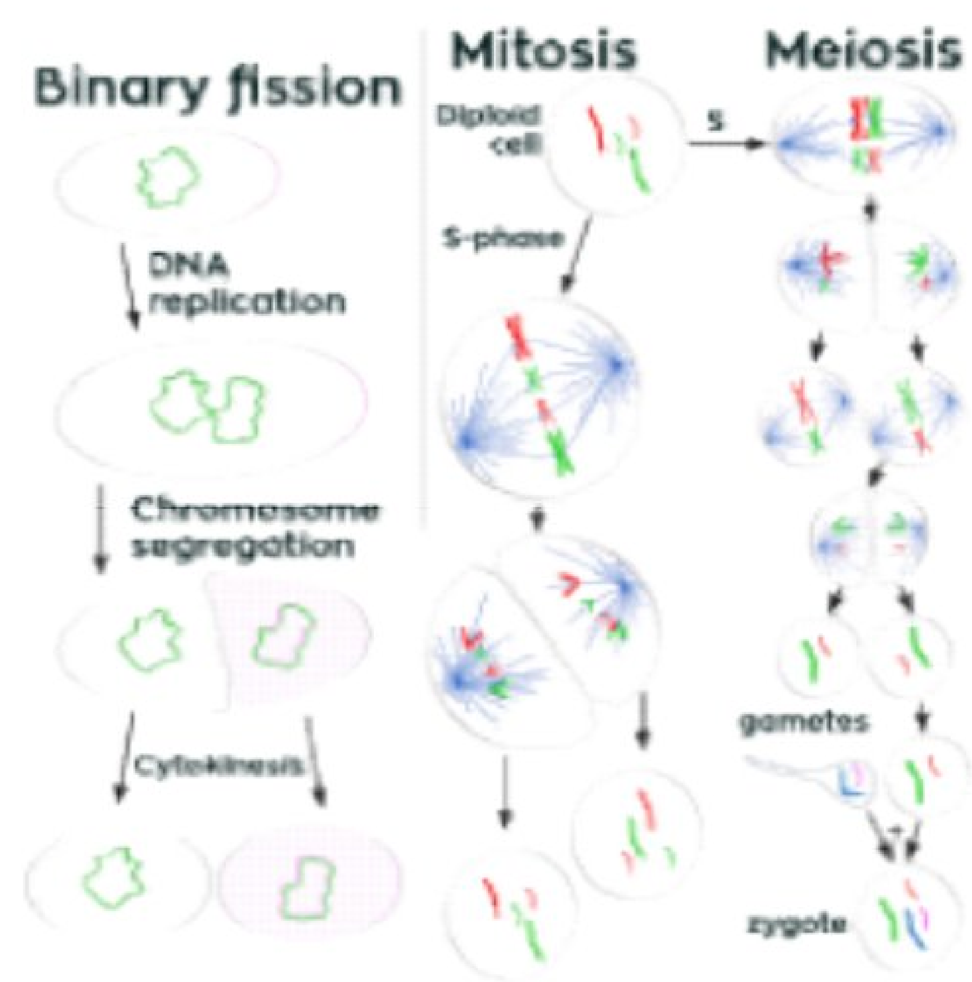

Many bacteria reproduce through binary fission, which is compared to mitosis and meiosis in this image. A culture of *Salmonella* A colony of *Escherichia coli*[111]

Unlike in multicellular organisms, increases in cell size (cell growth) and reproduction by cell division are tightly linked in unicellular organisms. Bacteria grow to a fixed size and then reproduce through binary fission, a form of asexual reproduction.[112] Under optimal conditions, bacteria can grow and divide extremely rapidly, and some bacterial populations can double as quickly as every 17 minutes.[113] In cell division, two identical clone daughter cells are produced. Some bacteria, while still reproducing asexually, form more complex reproductive structures that help disperse the newly formed daughter cells. Examples include fruiting body formation by myxobacteria and aerial hyphae formation by *Streptomyces* species, or budding. Budding involves a cell forming a protrusion that breaks away and produces a daughter cell.[114]

In the laboratory, bacteria are usually grown using solid or liquid media.[115] Solid growth media, such as agar plates, are used to isolate pure cultures of a bacterial strain. However, liquid growth media are used when the measurement of growth or large volumes of cells are required. Growth in stirred liquid media occurs as an even cell suspension, making the cultures easy to divide and transfer, although isolating single bacteria from liquid media is difficult. The use of selective media (media with specific

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nutrients added or deficient, or with antibiotics added) can help identify specific organisms.[116]

Most laboratory techniques for growing bacteria use high levels of nutrients to produce large amounts of cells cheaply and quickly.[115] However, in natural environments, nutrients are limited, meaning that bacteria cannot continue to reproduce indefinitely. This nutrient limitation has led the evolution of different growth strategies (see r/K selection theory). Some organisms can grow extremely rapidly when nutrients become available, such as the formation of algal and cyanobacterial blooms that often occur in lakes during the summer.[117] Other organisms have adaptations to harsh environments, such as the production of multiple antibiotics by Streptomyces that inhibit the growth of competing microorganisms.[118] In nature, many organisms live in communities (e.g., biofilms) that may allow for increased supply of nutrients and protection from environmental stresses.[52] These relationships can be essential for growth of a particular organism or group of organisms (syntrophy).[119]

Bacterial growth follows four phases. When a population of bacteria first enter a high-nutrient environment that allows growth, the cells need to adapt to their new environment. The first phase of growth is the lag phase, a period of slow growth when the cells are adapting to the high-nutrient environment and preparing for fast growth. The lag phase has high biosynthesis rates, as proteins necessary for rapid growth are produced.[120][121] The second phase of growth is the logarithmic phase, also known as the exponential phase. The log phase is marked by rapid exponential growth. The rate at which cells grow during this phase is known as the *growth rate* (*k*), and the time it takes the cells to double is known as the *generation time* (*g*). During log phase, nutrients are metabolised at maximum speed until one of the nutrients is depleted and starts limiting growth. The third phase of growth is the *stationary phase* and is caused by depleted nutrients. The cells reduce their metabolic activity and consume non-essential cellular proteins. The stationary phase is a transition from rapid growth to a stress response state and there is increased expression of genes involved in DNA repair, antioxidant metabolism and nutrient transport.[122] The final phase is the death phase where the bacteria run out of nutrients and die.[123]

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